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CAMBRIDGE, MASS. 15 SEPTEMBER, 1969 NUMBER 326

ANOLIS INSOLITUS, A NEW DWARF ANOLE OF ZOOGEOGRAPHIC IMPORTANCE FROM THE MOUNTAINS OF THE DOMINICAN REPUBLIC

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and

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ABSTRACT: *Anolis insolitus*, a new dwarf species occurring in the Cordillera Central of the Dominican Republic, is closely related to both *A. occultus* known from several montane localities in Puerto Rico and *A. darlingtoni* of the Massif de la Hotte in Haiti, but is closer to *A. darlingtoni*, a much larger species. The three species are basal members of the *carolinensis* group (*sensu lato*) in the West Indies, of which *A. occultus* is the most primitive known member.

INTRODUCTION

In the spring of 1963, the Museum of Comparative Zoology received from the Cordillera Central of the Dominican Republic a single small anole that was immediately recognized by E. E. Williams and by James D. Lazell, Jr., as a very distinctive and important new species. Even at that time the name *insolitus* — "strange or unusual" — was chosen for it.

Because, however, the new species was represented by a single specimen, its description was delayed, to wait upon more material. An attempt by Lazell, during the last week of December of 1963 and the first week of January 1964, to collect at the exact locality where the first specimen was taken failed because of bad weather.

Not until late summer of 1968 did E. E. Williams and A. S. Rand succeed in visiting the pertinent locality and in collecting a small series that fully confirms the "unusual" nature of the animal,

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which also turns out to be of considerable phyletic and zoogeographic significance, its external indications of relationship verified by an osteological investigation made by Richard Etheridge (pers. comm.):

Anolis insolitus n. sp.

Type. MCZ 60144, Paraje La Palma, Sección La Palma, Municipio Constanza, Provincia La Vega, República Dominicana, C. E. Ray and R. R. Allen coll. 19 March 1963.

Paratypes. (Same locality as type) MCZ 107014-18, A. S. Rand and E. E. Williams coll. 30-31 July 1968. (MCZ 107015 skeletonized, MCZ 107017-18 used unsuccessfully for chromosome study.)

Diagnosis. A dwarf anole related on the one hand to *A. darlingtoni* Cochran of southwest Haiti, from which it differs in size and in several features related to size, e.g. lamellae under fourth toe), and on the other to *A. occultus* of the mountains of Puerto Rico (which it resembles in size but from which it differs especially in

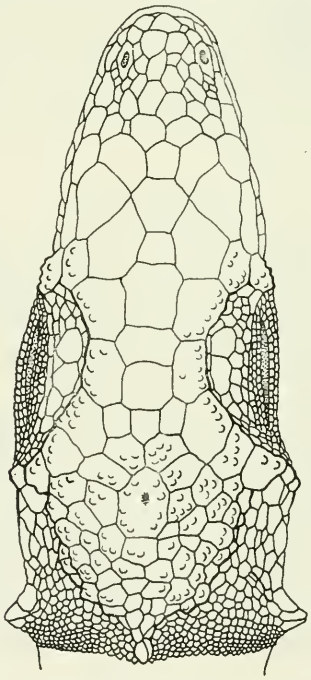

Fig. 1. *Anolis insolitus,* Type, MCZ 60144: dorsal view of head.

the much larger head scales). The new species differs from all known species of *Anolis* in the presence of small but distinct postorbital, supratemporal, and occipital spines, bony in nature and especially prominent in males (Fig. 1).

Description. Head: Narrow, elongate. Head scales large, smooth, smallest at tip of snout, three scales across snout between large second canthals. Nostril oval, nasal scale separated from rostral by a single oval scale. Rostral scale wide, low, in contact with five scales posteriorly.

Supraorbital semicircles large, weakly convex, rugose laterally, separated by a single row of scales as large or larger. A much less distinct row of seven large oval granules or scales on each side at the supraciliary margin, no elongate supraciliary. Posterior and internal to the supraciliary row, some smaller granules or scales. A single scale raised into a spine just beyond these smaller granules at the posterior end of each supraorbital semicircle. An elongate supraocular disk of ca. six to nine enlarged scales, two of them about one-third to one-half the size of the scales of the semicircles. Canthal ridge of six scales well defined, second canthal scale largest, diminishing in size anteriorly, anteriormost below nostril. Loreal rows three with some irregularity in size. A distinct supratemporal line of four to five enlarged scales, the fourth replaced by a spine. Temporal scales small, smallest at center, flat. Supratemporal scales above supratemporal line becoming larger toward a ridge of protuberant — almost spiny in ♂ — scales forming a U-shaped crest behind the interparietal region, in ♂ with a larger spine at base of U. Interparietal ovoid, much larger than the ear opening, separated by one flat scale on each side from the supraorbital semicircles. Scales surrounding interparietal large, flat, with some tubercles in ♂ (tubercles also on surrounding scales in ♂). Ear small, subround, placed far ventrally, directly behind the comissure of the mouth.

Suboculars in contact with supralabials, anteriorly grading into loreals, posteriorly grading into temporals. Seven supralabials to center of eye.

Mental large, semidivided, wider than deep, in contact with four granules between the infralabials. Two large infralabials on each side in contact with sublabials. Throat scales granular, smooth.

Trunk. Dorsal scales granular, smooth, subequal on flanks and middorsum except for a crest of small, triangular, swollen scales continuing middorsally from the U-shaped crest behind the interparietal to a point a little behind the insertion of the forelimbs.

Ventrals larger than dorsals, smooth, round, in transverse rows.

Gular fan. Moderately large; present in both sexes and well developed even in juveniles, lateral margins slightly inset, scales granular, smaller than throat scales, much smaller than ventrals; lateral scales about as large as edge scales in well-separated rows (♀) or less well-defined rows (♂).

Limbs and digits. Limbs short, tibial length ca = distance tip of snout to middle of eye. Fifteen to sixteen lamellae under phalanges ii and iii of fourth toe. Scales of limbs smooth, those of anterior thigh larger than those of ventrals. Supradigital scales smooth.

Tail. Round, with a distinct dorsal crest of a median row of enlarged, keeled scales, interrupted at intervals of two to four scales by paired paramedial scales, usually the most distal scale in any small series largest but with some irregularities. No enlarged postanals, but scales nearest vent larger in ♂ than ♀. Scales behind vent and round base of tail smooth, grading into keeled scales distally. Four ventral rows distinctly enlarged.

Color in life. The general body color is greenish or grey-brown, mottled, lichenate, with the dewlap, present in both sexes, blue-grey in front, orange behind. Detailed notes on two specimens follow: (1) ♀. Dull green with a dark grey middorsal zone enclosing a series of dark grey spots. Traces of a sacral butterfly pattern overlying a dull orange sacral spot. Blurred barring on tail, barring hardly visible on limbs. A light yellow streak under eye; reddish color on upper eyelid. Faint indication of a light streak from ear to arm. Flanks mottled. Dewlap blue-grey anteriorly, dull orange posteriorly, crossed by rows of white scales. (2) ♂. Dark butterfly-shaped blotches dorsally, less distinct on sides. One such blotch above shoulders, two on back, and one on sacrum. The sacral blotch crossed by a light orange spot. Tail and limbs crossbarred. A light yellow streak under eye; skin around eye reddish. A curved yellow streak from above ear to above base of arm. Sides and belly lightish cream, lightly speckled laterally with brown. Dewlap as above.

Field observations. (Compare with observations on *A. occultus* by Webster, 1969). Four of five specimens were caught asleep. One adult was taken about six feet from the ground on a broad, nearly horizontal leaf of a bush, its head facing toward the stem. Two other adults were found eight to ten feet apart, sleeping along slender, nearly horizontal twigs of bushes. One was about four and the other about five feet above the ground. Two juveniles were found at the edge of the forest about 15 feet apart, sleeping

Fig. 2. *Anolis insolitus*, Type, MCZ 60144: lateral view.

along the very slender terminal twigs of bushes; one was about six and the other eight feet up.

The single adult seen during the day was eight feet up on a horizontal, quarter-inch branch of a small tree. It was in a rather open part of the forest on a sunny morning. It moved in and out of sun flecks, apparently paying little attention to them in the few minutes that it was watched. At first it pressed itself against the branch and squirrelled to the other side. Its mottled pattern matched the lichen-covered branch, and it was hard to see. Soon it resumed a more erect posture and slowly climbed along one branch and out on one even more slender. When an attempt was made to catch it, it ran along this branch and jumped to another a few inches away. When captured, it threatened with open mouth and erected the blue-grey and orange dewlap.

Behavior (A. S. Rand). On the morning after capture, the following observations on the locomotion and defensive behavior of two specimens were made: on the ground or along a perch, movement was either a slow, very deliberate walk or a series of rapid hops. Jumps from perch to perch were made willingly and accurately, and were of considerable distances for a two-inch lizard. One jump measured about 12 inches with little loss in height; another jump was six inches, and the lizard landed on a perch higher than that from which it started.

A lizard climbs willingly and without difficulty on small twigs but seems more at home on twigs of about body diameter than on those much smaller. When it is approached by a hand, a lizard will squirrel slowly around its perch, even a slender one, pressing its whole length against the substrate. On a horizontal branch the lizard may go completely underneath. Very closely approached, it may jump away or to the ground. When seized, the mouth is opened threateningly, and there is an attempt to bite.

Except when hiding, the head and shoulders are raised away from the substrate, and the neck is straight, whereas the vent is almost, but not quite, in contact with the substrate.

In walking, the toes of the fore feet are spread widely so that toes 1 and 5 point in approximately opposite directions. On very slender perches the toes oppose one another: 1, 2 versus 3, 4, 5 or 1, 2, 3 versus 4, 5.

On flat surfaces, the toes of the hind feet spread so that toe 4 extends the axis of the foot, toe 5 is at right angles to this behind, toe 1 at right angles in front, and 2 and 3 between. On slender perches, sometimes toe 5 opposes the others, sometimes 1 and 5

together oppose 2, 3, 4. The tail is frequently carried in an upright curve, but is more often straight and rests against the substrate. While climbing, the tail is frequently used as a sliding hook. Usually at about half way along its length, the tail hooks in a semicircle over and behind some projection. As the lizard moves forward, the hook slides backwards along the tail until the tip of the tail reaches the projection, crosses it, and drops off. The tail may be used on a straight branch without projections by being bent to one side and around the branch. If the branch is shaken, the tail may strengthen its hold by forming a complete loop around the branch. Apparently only the very tip is flexible enough to grip a small branch tightly.

Relationships. Anolis insolitus is almost as distinct in Hispaniola as *A. occultus* is in *Puerto Rico* (Williams, Rivero, and Thomas, 1965): it is quite impossible to confuse it with any other Hispaniolan species. However, it does have resemblances in two directions, with *A. darlingtoni* of western Hispaniola and with *A. occultus* of the mountains of Puerto Rico. These resemblances indicate that it is an annectant rather than an isolated form.

It is best placed in its proper group on osteological characters. Table 1 records the pertinent comparisons (information provided by Richard Etheridge — pers. comm. — from X-rays of *occultus, insolitus,* and *darlingtoni* and from dry skeletons of *occultus* and *insolitus*). According to the informal groupings suggested by Etheridge (1960), *A. occultus* emerges as a very primitive (and somewhat aberrant) member of the *carolinensis* group (those with "T-shaped" interclavicles; compare Etheridge's 1960, fig. 4) of alpha anoles (those without caudal transverse processes) . The primitiveness of *occultus* is manifested by a high number of attached inscriptional ribs ("parasternals" of Etheridge 1960, but see Etheridge 1965). *A. darlingtoni* is a somewhat less primitive member of the same group (fewer attached inscriptional ribs), but is peculiar in the specialized character of non-autotomic caudal vertebrae. *A insolitus* is again a member of the same group, but, like *A. darlingtoni,* is specialized in having non-autotomic caudals; it is, however, more advanced than *A. darlingtoni* in having only three attached inscriptional ribs and one free one. (Most of the *carolinensis* group show the latter condition; a few are still more advanced and have only two attached inscriptional ribs and two free.)

A. insolitus has pterygoid teeth. These are absent in *A. occultus,* and we lack information about *A. darlingtoni.*

The occurrence of pterygoid teeth (primitive for lizards in general) in *Anolis* is somewhat erratic. They are usually absent in dwarf species. At least in the West Indies, however, they are frequently present in the more primitive members of any group. In the *carolinensis* group, their presence can be verified in *A. chlorocyanus, A. coelestinus, A. aliniger, A. equestris, A. allisoni,* and *A. carolinensis* among the more primitive species, and in *A. lucius* among more specialized forms. The presence of pterygoid teeth in *A. insolitus* is presumably to be regarded as primitive and is so recorded in Table 1.

A. darlingtoni and *A. insolitus* are unique among Hispaniolan anoles in having non-autotomic caudals, and, indeed, are the only West Indian members of the genus *Anolis* that lack tail autotomy. (*Chamaeleolis* and *Chamaelinorops,* the only other West Indian anoles to lack tail autotomy, are very distinct genera.) Though loss of autotomy has occurred several times in anoles, its occurrence in the West Indies only in two species on one island suggests affinity; it does not, of course, demonstrate it.

The enlarged plate-like head scales of *A. insolitus* and *A. darlingtoni* (compare Fig. 3 and Fig 2) provide the most obvious external resemblance between the two species. This character, however, is not unique to these species even within the West Indies. In fact, *A. darlingtoni* and *A. valencienni* were formerly united in the genus *Xiphocercus* solely on the basis of similar large plate-like head scales. *A. darlingtoni* and *valencienni,* however, belong to

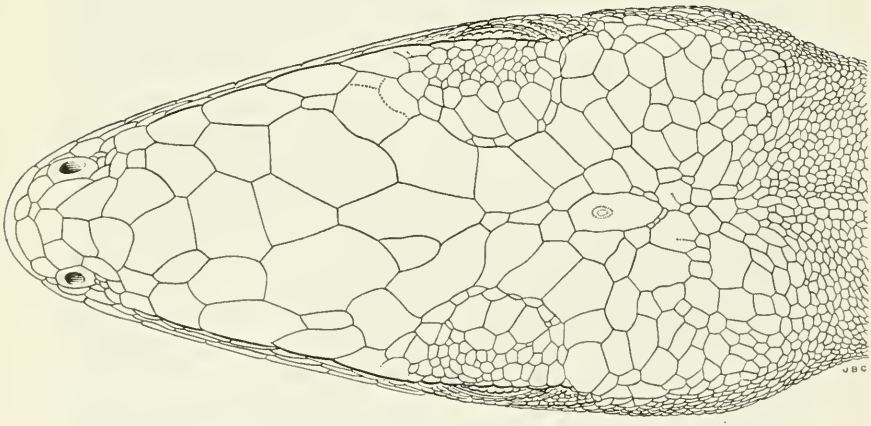

Fig. 3. *Anolis darlingtoni,* MCZ 38251: dorsal view of head.

two different sections of the genus *Anolis* as analyzed by Etheridge (1960), alpha and beta respectively, and the character of plate-like head scales is now recognized as having arisen many times within the anoles. Again, therefore, this resemblance is not proof of affinity between *darlingtoni* and *insolitus,* but the presence of so special a character in two species of one island is suggestive.

It would be a possible argument against the close affinity of the two species that *darlingtoni* (72 mm) is approximately twice the snout-vent length of *insolitus* (33 mm). Differences in size between closely related species, particularly if they are sympatric, are not unusual, but as far as is known, these two species are widely allopatric, and the size difference is extreme.

However, a number of external characters suggest not only an affinity between *darlingtoni* and *insolitus* but also suggest relationships with *occultus:* (1) the simple annular nasal scale separated by one round scale from the rostral (=prenasal not fused with nasal); (2) the small, round, ventrally-placed ear; (3) the long head and short limbs; (4) the low number of loreal rows; (5) the smooth ventrals.

Table 2 lists not only those characters in which all three species are similar but also all other pertinent external characters. The significant resemblances between any two or among all three species are italicized. It is easily seen that *insolitus* occupies a key position. In many critical and sometimes quite special characters (e.g. absence of an elongate supraciliary scale; presence of a *slotted* gular fan in both sexes), *insolitus* resembles sometimes *darlingtoni,* sometimes *occultus.*

It is clear, of course, that *insolitus* is not just an intermediate between the two species. It has very striking specializations of its own. The small spines and rugosites on the head are the most remarkable feature; these are as visible on the skull as they are externally. The crest of enlarged scales on the nape and the peculiar tail crest are almost as singular. In another regard, *insolitus* is not intermediate; the inscriptional ribs show a condition more advanced than that shown by either *occultus* or *darlingtoni.* However, such a complex of primitive and advanced adaptations is just what we should expect of the surviving representative of the stock that was at one time intermediate between the ancestral grade now represented by *occultus* and the more advanced grades represented by *darlingtoni* and by other still more advanced members of the *carolinensis* group. The importance of *insolitus* as an annectant form phyletically and zoogeographically is not diminished by admission of its specializations.

Figure 6 shows the known localities for *A. darlingtoni* (still known only from the unique type from Roche Croix, Massif de la Selle, Haiti) and *A. insolitus* (known now from six specimens from La Palma in the Cordillera Central of the Dominican Republic). Such a map reflects more ignorance than knowledge. Though Hispaniola has recently been assiduously collected, it is obvious that the fund of new information and of new taxa is not nearly exhausted, and the need for further collection and study is abundantly clear. The genus *Anolis* is only one fraction — even though an important one — of the herpetofauna of Hispaniola. The current count of species (including *insolitus*) is 21. Of these, no less than seven have been described in the last ten years (*christophei* Williams; *koopmani* Rand; *cochranae* Williams and Rand; *whitemani* Williams; *singularis* Williams; *rimarum* Thomas and Schwartz; *insolitus* Williams and Rand). In Table 3 we list the known species with comment on degrees of distinctness and on geographic variation (the latter may in some cases conceal valid species). We confess to a lack of belief that the list is complete. An asterisk marks those species that are especially inadequately known.

Certainly the most plausible assumption based on current evidence is that *darlingtoni* and *insolitus* are geographic representatives — south island and north island respectively — of one stock. This assumption, however, leaves the extreme size disparity of these allopatric species without easy explanation. A discussion of this point and of the possible history of Hispaniolan anoles is deferred to a future paper.

A. darlingtoni has not previously been adequately figured. Cochran (1941, pl. 11) provided only a photograph, which showed little more than general shape. Figures 3 and 4 permit comparison with the similar figures of *A. insolitus*.

Figure 5 diagrams the probable relationship of *A. insolitus* within the *carolinensis* subsection of alpha *Anolis*. It and *A. darlingtoni* appear to be the earliest radiation of this stock within Hispaniola. Three further radiations have occurred within Hispaniola, one of these, that of the Hispaniolan grass anoles, being the result of a back invasion from the complex radiation of the *carolinensis* group in Cuba (Williams, 1961).

ACKNOWLEDGMENTS

This study was partly supported by National Science Foundation grant GB 6944 to E. E. Williams. Figures were prepared by Joshua Clark and by Laszlo Meszoely.

Fig. 4. *Anolis darlingtoni*, MCZ 38251: lateral view.

TABLE 1

	occultus	*insolitus*	*darlingtoni*
angular	absent (SPECIALIZED)	same	? same
splenial	absent (SPECIALIZED)	same	? same
pterygoid teeth	absent (SPECIALIZED)	present	?
interclavicle	T-shaped (SPECIALIZED)	same	same
inscriptional chevrons	5-6 attached; 0 free (PRIMITIVE)	3 attached; 1 free (SPECIALIZED)	4 attached; 0 free (INTERMEDIATE)
caudal vertebrae	1. without transverse processes	same	same
	2. autotomic (PRIMITIVE)	non-autotomic (SPECIALIZED)	non-autotomic (SPECIALIZED)

TABLE 2

occultus	*insolitus*	*darlingtoni*
34 mm snout-vent length	33 mm snout-vent length	72 mm snout-vent length
9-13 scales across snout	3 scales across snout	5 scales across snout
nasal scale separated from rostral by a single scale	*nasal scale separated from rostral by a single scale*	*nasal scale separated from rostral by a single scale*
supraorbital semicircles weak, separated by 2-4 scales	supraorbital semicircles strong, separated by one row of *wide* scales	supraorbital semicircles strong, separated by one row of narrow scales
No differentiated supraciliaries	*A distinct supraciliary row, but no scale elongate*	*A distinct supraciliary row, but no scale elongate*
no postorbital, supratemporal, or occipital spines	postorbital, supratemporal, and occipital spines, especially prominent in males	no postorbital, supratemporal, or occipital spines
no distinct supratemporal line of enlarged scales	a distinct supratemporal line of large scales *ending in a spine*	no distinct supratemporal line of enlarged scaled
Ear small, round, low	*Ear small, round, low*	*Ear small, round, low*
interparietal small, round, ca = ear, separated from semicircles by 2-6 scales	*interparietal ovoid, much larger than ear, separated from semicircles by one large scale*	*interparietal ovoid, much larger than ear, separated from semicircles by one large scale*
canthal ridge weak, barely differentiated	canthal ridge strong	canthal ridge strong
loreal rows 2-6	*loreal rows 3*	*loreal rows 3*
suboculars in contact with supralabials	*suboculars in contact with supralabials*	*suboculars in contact with supralabials*
10-11 supralabials to center of eye	7 supralabials to center of eye	7 supralabials to center of eye
mental in contact with 4 scales between sublabials, no differentiated infralabials	mental in contact with 4 scales between well-differentiated infralabials	mental in contact with 2 scales between well-differentiated infralabials

occultus	*insolitus*	*darlingtoni*
middorsal scales smooth, flat, subequal	a low crest of triangular enlarged scales on the nape to a little past insertion of arms	scales on nape somewhat smaller than middorsally
ventrals > dorsals, smooth, juxtaposed in transverse rows	ventrals > dorsals, smooth, juxtaposed in transverse rows	ventrals ca = dorsals, smooth, subimbricate in transverse rows
gular fan large, present in both sexes; inset, scales in rows in females, not in row in males	*gular fan moderately large in both sexes, inset, scales in distinct rows in females, rows less distinct in males*	gular fan large, not inset, scales evenly distributed in males
limbs short, tibial length ca = distance snout tip to center of eye	*limbs short, tibial length ca = distance snout tip to center of eye*	*limbs short, tibial length less than distance snout tip to center of eye*
14-20 lamellae under phalanges ii and iii of 4th toe	15-16 lamellae under phalanges ii and iii of 4th toe	24 lamellae under phalanges ii and iii of 4th toe
scales of limbs smooth, always smaller than ventrals	scales of limbs smooth, of anterior thigh larger than ventrals	scales of limbs weakly carinate, of anterior thigh larger than ventrals
supradigital scales smooth	*supradigital scales smooth*	supradigital scales multicarinate
tail round without dorsal crest	tail round with dorsal crest	tail round without dorsal crest
no enlarged postanal scales in male	*no enlarged postanal scales in male*	enlarged postanal scales in male

TABLE 3

The Anoles of Hispaniola

Species	*Distribution*	*Distinctness*	*Geographic differentiation*
ricordii	islandwide	in a separate species group	Several described subspecies, some of which are sharply enough distinct to raise the question of possible species status
**insolitus*	known from one north island locality	very sharply distinct, but apparently the north island representative of *darlingtoni*	unknown
darlingtoni	known from one south island locality	amply distinct, the south island representative of *insolitus*	unknown
coelestinus	south island	distinct, overlapping its north island representative *chlorocyanus* in a very limited fashion in the Port-au-Prince region, perhaps at other points of contact	present but not strongly marked
chlorocyanus	north island	almost parapatric to its south island representative *coelestinus* but with limited overlap	present but not strongly marked

Species	*Distribution*	*Distinctness*	*Geographic differentiation*
aliniger	north island with one known incursion into south island	amply distinct from both sympatric *chlorocyanus* and its closer relative *singularis*	unknown
singularis	south island and Gonâve	amply distinct both from sympatric *coelestinus* and its closer relative *aliniger*	unknown
cybotes	islandwide except peaks of the Cordillera Central and some of the arid plains	distinct, one of a group of climatically differentiated species	mostly not strongly marked but some distinct altitudinal (*armouri*) and peripheral races (*haitianus*). Some still unanalyzed local populations
whitemani	certain extreme arid areas of both north and south islands	distinct, the arid country representative of *cybotes*	unknown
shrevei	peaks of the Cordillera Central	distinct, the representative of *cybotes* at extreme altitudes, structurally close to *whitemani* but very distinct ecologically	unknown
distichus	most of the island, usually in mesic situations	distinct, but closely related to its arid country representative *brevirostris*	striking color races, especially remarkable diversity in dewlap color

brevirostris	arid portions of north and south islands and Gonâve	distinct, climatically separate from its close relative *distichus* but with some marginal sympatry	dewlap races present
hendersoni	south island	sharply distinct, related to *chlorocyanus-coelestinus* but not closely	strong color races
christophei	north island (montane broadleaf forest)	sharply distinct, related to *monticola-rimarum* but not closely	unknown
etheridgei	north island (montane broadleaf forest)	sharply distinct, related to *monticola-rimarum* but not closely	unknown
monticola	south island (montane broadleaf forest)	distinct, but the south island representative of *rimarum*	two color races
**rimarum*	known from a single north island locality (montane broadleaf forest)	distinct, but obviously close to *monticola*	unknown
**koopmani*	known from one south island locality (montane broadleaf forest)	amply distinct, related to *monticola* but not closely	unknown

Species	*Distribution*	*Distinctness*	*Geographic differentiation*
semilineatus	islandwide	distinct, the mesic climatic representative of arid area *olssoni* to which it is partly sympatric	no indication of geographic differentiation
olssoni	islandwide but not known from the south coast of the south island	distinct, the dry country representative of mesic area *semilineatus*	no indication of geographic differentiation
**cochranae*	higher elevations of the Cordillera Central	distinct; an altitudinal derivative of the *semilineatus* group	unknown

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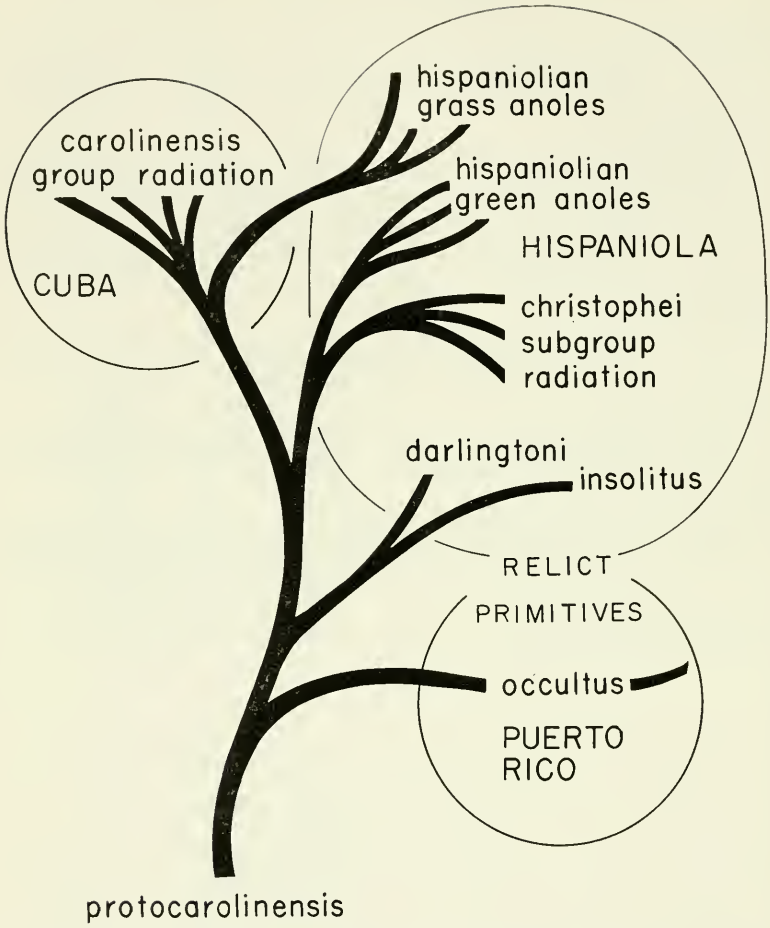

Fig. 5. Diagram of relationships within the *carolinensis* subsection of alpha *Anolis*. *A. darlingtoni*, *A. insolitus*, and *A. occultus* are primitive relicts within this subsection.

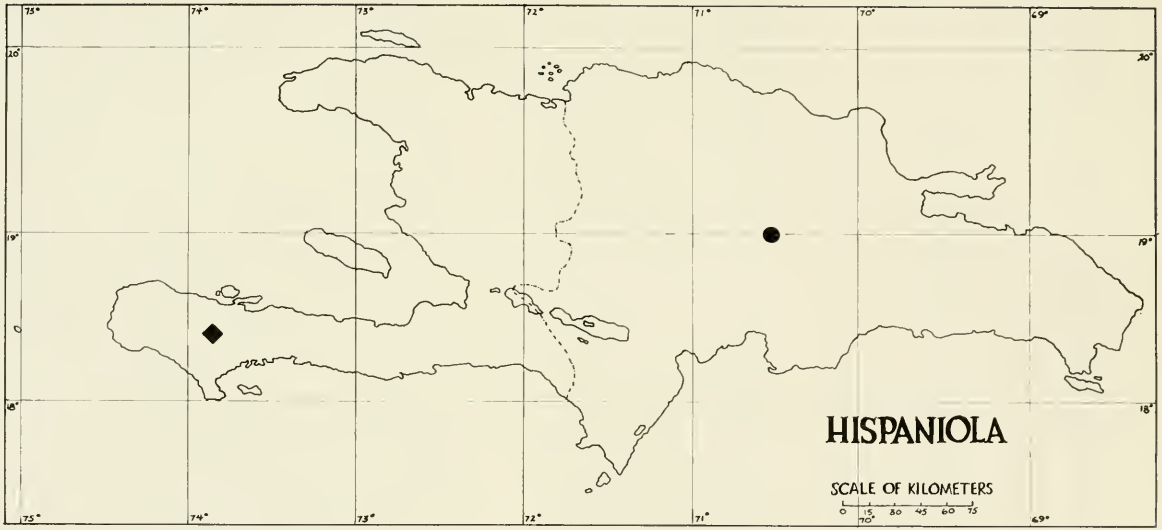

Fig. 6. Map of the distribution of *A. insolitus* and *A. darlingtoni*.

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CAMBRIDGE, MASS. 15 SEPTEMBER, 1969 NUMBER 327

THE ANOLES OF LA PALMA: ASPECTS OF THEIR ECOLOGICAL RELATIONSHIPS

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ABSTRACT. The ecological relationships of the anoles known from a locality in the Cordillera Central of the Dominican Republic are described in terms of the climatic and structural habitats found useful in describing these relationships for the anoles of the Hispaniolan lowlands and of other West Indian islands. The montane fauna of the central Dominican Republic is closest both ecologically and phyletically to the montane fauna of the southwestern portion of Hispaniola. Discrepancies may be due to incomplete knowledge of these montane faunas, which have only recently been carefully collected. Both the Hispaniolan montane faunas are now relict, although locally occurring in dense populations.

INTRODUCTION

Reports of the ecological relationships of closely related sympatric species provide one of the basic lodes of raw material for studies of competition, adaptive radiation, and evolution. This paper, concentrating on a relict population of montane anoles in Hispaniola, is one of several describing the ecological relations among sympatric anoles at various places in the West Indies (e.g. Ruibal, 1961; Collette, 1961; Rand, 1962, 1964, 1967b; Rand and Rand, 1967; Schoener, 1967, 1968; Schoener and Gorman, 1968). It fills an important gap in the series and is preliminary to a study comparing the patterns of ecological adaptation shown by anoles in different areas and discussing their evolutionary significance.

The area we chose for study — La Palma in the Cordillera Central of the Dominican Republic — is one in which there are small relict patches of broad-leaf montane forest surrounded by

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cultural steppe. Though most of this type of forest has been cut all over Hispaniola, relicts like those at La Palma occur at a number of places. La Palma provided us with the opportunity to study the interrelationships of seven species of anoles, four of them montane and occurring in the relict forest, and three lowland, occurring primarily outside the forest. In this paper, we have concentrated on one locality instead of discussing relationships between montane and lowland anole faunas in general terms, because an approach in terms of a local fauna will allow the reader to distinguish more clearly our factual information (i.e., what we saw) from our ideas about what probably happens.

Our observations were made at La Palma during eight visits, two of them at night, on five days between 23 and 31 July, 1968. The brevity of our observations and their concentration at one time of year limits their generality, but they are much more extensive than any yet available for this specific montane situation, and, since there is little prospect of extending them in the near future, they are offered here.

Our La Palma observations have been supplemented by our observations at nearby areas and elsewhere in Hispaniola and by the unpublished observations of Drs. James Lazell, Clayton Ray, and Albert Schwartz, to whom we are grateful.

We are deeply indebted to Dr. E. de J. Marcano and his associates and family for their help and kindness in the Dominican Republic. Dr. Marcano's enthusiasm and generosity in helping visiting scientists are extraordinary, and we have benefited largely.

This study was partly supported by National Science Foundation grant GB-6944 to Ernest E. Williams.

GENERAL REMARKS AND DEFINITIONS

Our study at La Palma was undertaken in order to determine the ecological relationships of the anoles sympatric there. Since the data are intended for comparison with earlier studies at other localities, we have tried no new methods. We have assumed that careful censusing of microhabitats (structural and climatic niches, see below) and a record of adult size will give a sufficient approximation of the most important ecological relationships between the species. As an aid to future workers, and because of their relevance to interspecific social behavior, we have also noted general appearance and dewlaps. (A comment on the signal significance of dewlaps is being published elsewhere.)

Structural and climatic habitats. These terms are used in the senses previously defined (Rand, 1964, 1967b; Schoener, 1967, 1968). Structural habitat refers to that aspect of the microdistribution of an anole that can be described in terms of the physical structure of the environment. It is recorded as the height, diameter, and other characteristics of the perch used during the day, with mention of the normal foraging areas.

Climatic habitat describes an anole's relation to temperature and moisture in the environment. It is usually described in terms of light and shade distribution without reference to moisture. Observations on basking behavior are noted here. Earlier papers on anoles (Ruibal, 1961, and Rand, 1964) suggested that the most important factor in determining the climatic distribution of anoles was temperature, and certainly lizard body temperatures taken with a Schulteis thermometer correlate well with the light and shade aspects of the climatic habitat occupied. Even in the early papers, however, it was realized that humidity might be very important, and our observations and some experimental work of Sexton and Heatwole favor this. Sexton and Heatwole (1968) have shown that forest anoles in Panama lose water much more quickly under conditions of desiccation than do open-country anoles.

For both structural and climatic habitat some standardization of terms has been found useful:

Within the aspect of anole adaptation to structural habitat there are several types of anoles recognizable in terms of the perch area or areas on which *at least adult males* spend most of their active day. Such types are:

Crown anoles: anoles, typically of very large size, that are most frequently seen very high in trees, i.e., within the crown.

Twig anoles: dwarf anoles characteristically lying along thin branches and twigs, often near or in the crown.

Trunk-crown anoles: anoles usually found on the upper trunks of trees or in the crown.

Trunk anoles: anoles mainly confined to tree trunks and rarely climbing to the crown or descending to the ground.

Trunk-ground anoles: anoles found on the lower trunks of trees, foraging from there onto the ground.

Grass-bush anoles: anoles whose characteristic perch is on grass stems and bushes, away from trees. (This type of habitat is sometimes subdivided, and there may thus be grass anoles and bush anoles.)

Within the concept of climatic habitat, the convenient terms for the anoles adapted to the several habitats are sun anoles, half-shade anoles, and shade anoles. These must be used, however, with the express caveat that the situation in terms of insolation is not nearly as simple as these terms imply and that moisture, as suggested above, is of very real, perhaps primary, importance. Sun anole, half-shade anole, or shade anole imply only that the species so designated are most frequently (but *not* always) found in sunny situations, or in half or full shade.

A particular point must be made of the fact that observation of a single individual in sun or shade at a particular moment is not primary evidence of climatic habitat nor of basking behavior. Basking behavior must be defined as deliberate movement into a spot of sunlight, movement with the sunlight, and special postures associated with being in the sun. Non-basking animals may avoid sunny areas or move into and out of them almost randomly.

LA PALMA DESCRIBED

The specific area studied is adjacent to the tiny village of La Palma (ca. 800 meters) about 12 km east of El Río on the road to Bonao, La Vega Province, Dominican Republic. The small stream crossing the road here is clear, fast moving, and rocky, with a succession of pools and riffles about six to ten feet wide and shallow enough to be waded.

We worked upstream in the small patches of forest that bordered the stream. The area most thoroughly worked is up to 50 yards wide between the stream and a trail roughly paralleling it. This area extends about 200 yards from the road to the first crossing of trail and stream. Though the forest here had been hacked at, it had probably never been completely cleared at any time. Small trees form a nearly complete canopy 15 to 30 feet tall with a few open, swampy spots with only three- to five-foot high dense vegetation. There are scattered emergent trees 30-50 feet tall. These larger trees are most common and closest together along the banks of the stream.

Undergrowth is moderately dense in most places and, in addition to saplings and bushes, includes tree ferns, smaller ferns, and nettles. Vines are common but do not form vine curtains in most places. Movement is possible in any direction along the small paths or, except for a few dense fern patches, by following a winding course. Some moss and many lichens occur on tree trunks.

Bromeliads are only moderately common. The ground is nearly completely covered by a shallow leaf litter, much scratched, particularly near the main road, by chickens.

Above the first ford, in the area between the stream and the trail, the undergrowth had been cleared and coffee planted between large trees retained as shade.

Along much of the trail beyond the first ford there are fences and frequent dense fern thickets. In one place an outcrop of rock briefly replaces the fence on one side. Away from the stream and beyond the fences, the slopes are covered with pasture, or are under cultivation for beans in places. High on the ridges are bits of forest and scattered pine.

During one day we followed the trail for several kilometers as it crossed and recrossed the stream. The conditions of the first area repeated themselves until, beyond the small savanna settlement, even this gallery forest disappeared.

THE ANOLES

Table 1

Seven species of *Anolis* are known from the area of La Palma in the Cordillera Central of the Dominican Republic, making this among the richest in anole species of any area of comparable size in the West Indies. All species are restricted to Hispaniola except one (*A. distichus*), which also occurs in the Bahamas. Three species are widespread and quite well known in the lowlands (*A. distichus, A. cybotes, A. ricordii*) (Mertens, 1939; Rand, 1962). The remaining four are montane species, much more restricted in distribution and much less well known (*A. aliniger*) (Williams, 1965a); *A. christophei, A. etheridgei* (Thomas and Schwartz, 1967); *A. insolitus* (Williams and Rand, 1969). Two species (*A. chlorocyanus,* primarily lowland, and *A. cochranae,* strictly montane) that have not been found at La Palma are known from the general area and might occur at La Palma.

As mentioned above, the La Palma anoles fall into two natural groups, those known only from montane areas and those that also have a very wide lowland distribution. Three of the four montane species are primarily forest forms, the fourth may also occur in the forest but is certainly tolerant of open conditions, since it was under these conditions that it was taken at La Palma. Two of the three lowland species occur principally in the open, the third certainly occurs in the forest but is probably tolerant of relatively open situations.

TABLE 1

	Adult Size		*Structural Habitat*	*Climatic Habitat*
A. ricordii	very large	> 100 mm	on branches high in tree crowns	in and out of forest
A. insolitus	small	ca 40 mm	on twigs and small branches, understory ? and crown ?	in forest
A. christophei	medium	ca 50 mm	tree trunks	in forest
A. etheridgei	medium	ca 45 mm	slender perches and ground	in forest
A. aliniger	medium	ca 50 mm	branches, upper trunk, and crown	in forest and on edge
A. chlorocyanus	large	ca 70 mm	branches, upper trunk, and crown	in open
A. distichus	medium	ca 50 mm	trunks of trees	in open
A. cybotes	large	ca 60 mm	slender and moderate perches and ground, near thickets	in open
A. cochranae	small	ca 40 mm	grass, slender perches near ground	in open

MONTANE SPECIES

Anolis insolitus. A small species (ca 40 mm snout-vent length) gray or green, more or less distinctly mottled. Dewlap large in both sexes, skin blue-gray anteriorly, dull orange posteriorly, crossed by well-separated rows of white scales.

This recently described species (Williams and Rand, 1969) is known at present only from La Palma, where we found five animals in the forest.

The one seen during the day was about eight feet up on a slender branch of a small tree. It climbed along slender branches and hopped from one to another. It made no obvious efforts to seek or avoid the sun while we watched it.

In structural habitat, *A. insolitus* appears to be clearly a twig anole. In climatic habitat, it appears to prefer half-shade. In both respects, it strongly resembles *A. occultus* of Puerto Rico and probably resembles *A. isolepis* of Cuba (R. Ruibal, pers. comm.). It is not unlike young *A. valencienni* in Jamaica. The extent of ecological similarity to its much larger close relative, *A. darlingtoni* of southwestern Haiti (Williams and Rand, 1969), is unknown.

Anolis christophei. A medium-sized species (a little under 50 mm snout-vent length), brownish or greenish, conspicuously marked with dark dorsal butterflies, a pair of conspicuous light spots on the flanks and a light yellow or green mark under the eye. Dewlap very large in male, the skin light purplish gray, crossed by distinct rows of light scales. Dewlap very reduced in female.

This species, widely distributed at moderate to high elevations in the Cordillera Central and occurring also in the Cordillera Septentrional (Thomas and Schwartz, 1967), occurs at La Palma throughout the forest and occasionally on the edge, and also on the shade trees in coffee plantings. Usually it was in shade but occasionally in a sun fleck. No basking behavior was seen.

It perched on the trunks of trees, from saplings to very large trees. When smaller perches were used, these were typically next to a big tree or steep bank. Some individuals were seen on vertical earth banks along a stream and others on damp, vertical walls of a small outcrop. No close association with complex fissured tree trunks (such as that characteristic of *A. lucius* in Cuba, Ruibal, 1964) was evident. Most individuals were between two and twenty feet up; none were seen to go to the ground.

In structural habitat, *A. christophei* appears to be a trunk anole, as is *A. distichus,* but the latter occurs at La Palma in the open instead of in forest shade.

Anolis etheridgei. A medium-sized species (a bit less than 45 mm snout-vent length). Males plain greenish brown or with darker cross banding (we do not know if one male can show both). Females polymorphic with a highly variable dorsal pattern of stripes and spots. Dewlap in male of moderate size, the skin medium gray with evenly spaced whitish scales. Dewlap in female much reduced.

This species, restricted so far as known to higher elevations in the Cordillera Central, occurs at La Palma both inside the forest and at the edge. Almost all those seen were in shade; there was no suggestion of basking.

Almost all individuals were on slender perches (i.e., branches, twigs, fern stems, etc.) close to the ground; they perhaps come regularly to the ground. Many seem to live in dense bushes and fern thickets, since they were occasionally seen at the edges of these during warm, sunny periods and were commonly taken sleeping on them at night.

In structural habitat *A. etheridgei* is a bush anole, resembling *A. krugi* of Puerto Rico and, like that species, it prefers at least moderate shade. It also resembles, and is more closely related to, *A. hendersoni* of southern Hispaniola (Williams, 1963a).

Anolis aliniger. A medium-sized species (ca 50 mm snout-vent length). Green with the capacity to turn brown. Dewlap extremely reduced in both sexes. Perhaps replacing it in display is an orange area in the axilla followed by a black spot. Both markings are larger and brighter in the male.

This species is poorly known, although records indicate a wide distribution at moderate to high elevations in the Cordillera Central and across the Cul de Sac plain in the Massif de La Selle in Haiti.

The two specimens from La Palma were taken along the edge of the forest, one on a fence post in the sun, the other on a bush at night.

Very little is known about the ecology of this species, but from the very limited evidence, it may be a trunk-crown species of the montane forest, approaching the ground at forest edges.

A. aliniger is very closely related to *A. singularis* of southern Hispaniola, the behavior of which is even less understood than is that of *A. aliniger*. Both species are almost as closely related to the larger species *A. chlorocyanus,* which is a trunk-crown species of the lowlands known from near La Palma (Puenta Jimenoa, El Río) but not from La Palma itself. A fourth species, *A. coelestinus,*

is the geographic representative of *A. chlorocyanus* in southern Hispaniola (Williams, 1965a).

PRIMARILY LOWLAND SPECIES

Anolis ricordii. A very large species (over 100 mm snout-vent length), mottled gray and green. Dewlap large in both sexes, skin bluish gray in center, paling through light violet to pink at lower margin, edge with dense yellow-white scales.

This species occurs throughout Hispaniola, though with considerable geographic variation (Williams, 1962a, 1965b). It is primarily an inhabitant of the lowlands and is not known from high elevations.

At La Palma, one juvenile was taken about 10 feet up on a small branch of a small forest tree. Two adults were brought us from a large tree in a nearby agricultural area. It thus appears to occur here both in forest and in more open areas.

In other places in Hispaniola this is a crown species, as it probably is here. Whether or not this species basks is unclear, but it may well do so.

In its ecology, *A. ricordii* strongly resembles the other giant anoles, *A. cuvieri* of Puerto Rico and *A. equestris* of Cuba. It is a little less similar to the somewhat smaller *A. garmani* of Jamaica.

Anolis distichus. A species of moderate size (ca 50 mm snout-vent length) with considerable power of color change: green, gray, or brown; all light phases are finely mottled with darker. Dewlap in male of moderate size, with a rather wide, bright yellow border and bright red center. Dewlap reduced in female.

This species, which has many striking geographic color variants (Schwartz, 1968), occurs everywhere in Hispaniola except in situations of extreme aridity; it does occur at quite high elevations.

At La Palma, *A. distichus* is present in the open agricultural steppe and at the forest edge. We saw it also, but very rarely, in the forest. It is commonly seen sitting in sun flecks and seems to bask.

It perches on trees, frequently very large trees, and on fence posts, occurs at heights of one to twenty feet, and apparently does not regularly come to the ground.

A trunk anole like *A. christophei* in structural habitat, it differs in climatic habitat. The two overlap in microdistribution, but *A. christophei* is much more common in the forest and *A. distichus* in the open, each *almost* to the exclusion of the other.

Anolis cybotes. A large species (ca 60 mm snout-vent length). Brown with strong, dark, transverse dorsal markings and more or less distinct, light, longitudinal stripes on the flanks. Dewlap in male large, skin very pale yellow crossed by rows of similarly colored scales. Dewlap in females much reduced.

A. cybotes is a very common lowland species replaced in certain arid localities by its close relative *A. whitemani,* and in the highest areas of the Cordillera Central, by the related *A. shrevei.*

At La Palma, this species was seen in the open, at the forest edge and very rarely inside it. It is not as common here as *A. distichus* and seems associated chiefly with the edges of dense thickets in the open. One juvenile was seen in the forest on the ground.

In most areas, this is a trunk-ground species (Rand, 1961), common on trees and fence posts. Obvious comparisons then are with other trunk-ground species, such as *A. sagrei* on Cuba, *A. lineatopus* on Jamaica, and *A. cristatellus* on Puerto Rico. These comparisons are not so obvious at La Palma. The association with thickets and with the ground invites consideration of *A. etheridgei* as its forest counterpart. *A. cybotes* at La Palma is a bit anomalous and will be discussed further below.

DISCUSSION

The ecological picture seen in the anoles of La Palma requires discussion of three quite discrete topics, which we treat serially below:

1. The ecological significance of anole microdistributions. As has proved true of *Anolis* elsewhere, the anoles at La Palma differ from one another ecologically in obvious and striking ways. Here, as on other islands, the most conspicuous differences involve (1) size, which implies differences in size of food taken (Schoener, 1967); (2) structural habitat (i.e. size and height of typical perch and associated foraging area); and (3) climatic habitat (at La Palma, the differences between inside and outside the forest). These last two imply differences in foraging area.

Taken together, these three parameters specify a different but not exclusive feeding habitat for each species — not exclusive, because significant overlaps exist among species: a large species is small when young; both forest and open-country species occur together at the forest edge, and each invades, though only rarely, the climatic habitat of the others; finally, individuals of each species sometimes use quite atypical perches. Despite these overlaps, the

central portion of the food resources of each species seems unique to it.

The patterns of differences among sympatric anoles seen at La Palma are those usual in all well-analyzed situations in *Anolis:* structural habitat differences among anoles with the same climatic habitat; parallel structural habitats among animals with different climatic habitats; size as a reinforcing factor for either of these ecological patterns.

It is more usual than not for anole species to be constant, or nearly so, in their ecology throughout their ranges. The example of *A. cybotes* at La Palma reminds us, however, never to assume this out of hand. *A. cybotes* at La Palma is more nearly a bush anole than the trunk-ground anole it is over most of Hispaniola. Why it should have diverged in this fashion at La Palma is not clear, but it is clear that the only stringent ecological constraint on any species is that its ecological specializations be relevant and adequate in the specific biotic context in which it finds itself. Beyond this, restraints upon divergence are genetic: the possibilities for genetic change present in the genome of the animal, this genome being the product of prior history, i.e., the selective stresses of other times or places.

2. *The relationships of the montane faunas.* The most distinctive montane anole fauna in the West Indies is that of Hispaniola, and this is at present best known from the northern section of Hispaniola (the "north island" in the sense of Williams, 1961).

Four montane species are found at La Palma; three additional montane species, known from the Cordillera Central, appear not to occur there. One, *A. rimarum* (Thomas and Schwartz, 1967), is known only from one forest locality in Haiti, where it coexists with *A. christophei.* It was described from a very specialized habitat (boulders of talus slope) that does not occur at La Palma. The two remaining species, *A. shrevei* and *A. cochranae* are inhabitants of more open country: *A. shrevei* is a *cybotes* relative living in pine forests at very high altitudes; apparently it nowhere occurs in broad-leaf vegetation, and it does not follow pine to lower elevations. *A. cochranae* is a grass anole of high elevations. It might occur in the La Palma area away from the forest, but it has not been taken despite considerable night collecting.

Three of the anoles of the montane broad-leaf forest of the "north island" (*A. christophei, A. etheridgei,* and *A. rimarum*) are all members of one phyletic group (Williams, 1962b; Thomas

and Schwartz, 1967). The fourth anole of the north island montane forest, *A. insolitus,* is not as close but is probably a derivative within Hispaniola of the stock ancestral to this group and to the *coelestinus-chlorocyanus* group (green anoles, Williams, 1965a). The other two montane anoles, *A. cochranae* (grass) (Williams and Rand, 1961) and *A. shrevei* (pine) (Williams, 1963b), are, in contrast, derivatives of two diverse stocks and are each more closely related to a lowland stock than to the animals of the montane broad-leaf forest.

The "south island" of Hispaniola also has a montane anole fauna, but there are almost no species in common between "north" and "south" islands. The sole known exception, *A. aliniger,* has obviously established a rather recent beachhead across the Cul de Sac plain in the Massif de La Selle in Haiti (Williams, 1965a).

The "south island" montane species are, with the possible exceptions of *A. aliniger* and *A. singularis,* all more or less shade, i.e., forest, animals. *One, A. monticola,* is a very close relative of *A. rimarum* and occupies a similar rock-ground habitat. Southern *A. darlingtoni* is close to *A. insolitus* but is much larger, and its ecology is unknown. (It is still known from a unique type.) *A. singularis* is the southern representative of *A. aliniger* but lacks the latter's bold axillary pattern. *A. hendersoni* is the southern ecological equivalent of *A. etheridgei* but is not phyletically close. *A. koopmani* (Rand, 1964) is a dwarf ground anole believed to be close to the *A. monticola, A. rimarum, A. etheridgei, A. christophei* group, but it has no known northern representative. On the other hand, there are no known "south island" representatives of *A. christophei* or *A. shrevei* or *A. cochranae.*

Table 2 summarizes our present knowledge of the montane anole faunas of Hispaniola and of their north-south relationships. A question necessarily arises as to the completeness of this knowledge. Is there really no southern representative of *A. christophei?* No northern representative of *A. koopmani?* The faunas have been separated long enough to have achieved species difference in the two areas; they might also be old enough to differ genuinely as faunas also. However, the total known montane anole fauna of Hispaniola is twelve species; of these, six have been described in the last ten years: *A. christophei,* Williams, (1960); *A. koopmani,* Rand (1961); *A. cochranae,* Williams and Rand (1961); *A. singularis,* Williams (1965a); *A. rimarum,* Thomas and Schwartz (1967); *A. insolitus,* Williams and Rand (1969). Very

little work has yet been done in the Massif de la Hotte at the extreme end of the southwest peninsula of Haiti. It is consequently very possible that species are yet to be discovered.

TABLE 2

MONTANE ANOLE FAUNAS IN HISPANIOLA

NORTH ISLAND	*SOUTH ISLAND*
A. christophei	
A. etheridgei	*A. (hendersoni)*
A. rimarum	*A. monticola*
A. aliniger	*A. singularis*
	A. koopmani
A. insolitus	*A. darlingtoni*
A. cochranae	
A. shrevei	

We thus cannot at the moment determine whether the differences we now appear to see between the montane faunas of the north and south islands are (1) historically real — i.e., the result of long separation between the two areas, or (2) ascribable to the accident of extinction following a relatively recent separation, or (3) only an artifact of our still imperfect knowledge of the pertinent (particularly south island) areas. Of these, the first seems the least probable.

However, even on our present knowledge the point is clear that the montane forest faunas of Hispaniola, excluding *insolitus* and *darlingtoni,* make a close phylogenetic unit that seems to have only distant relationships with other anoles both within and without Hispaniola. A larger but still genuine phylogenetic unit includes these forest forms with *insolitus* and *darlingtoni* and the green anoles. All of these, then, contrast with the other Hispaniolan anoles, which seem to represent several different phylogenetic groups with more or less close relationships outside Hispaniola.

Such a set of relationships implies differences in times of origin or invasion. The montane forest species are the end points of an old radiation within Hispaniola. The widespread lowland species, except for the green anoles (*chlorocyanus* group, Williams 1965a, related on the one hand to *insolitus* and *darlingtoni* and on the other to the montane forest species), are the results of more recent invasions of Hispaniola and have provided more recent and less extensive radiations within the island.

This postulated history of the fauna suggests that anoles have invaded Hispaniola and established themselves throughout both the open and disturbed habitats, for these are the current habitats of the widespread lowlands species (least true of *ricordii*). The older species tend to be established in the montane forests and to resist invaders there. This pattern is similar to that suggested by Wilson, 1959, 1961, for the Melanesian ants.

3. Relict habitats and relict populations. On a very recent time scale, the forest at La Palma is a relict habitat and contains a relict of a once much more widely distributed and, as just suggested, probably old anole fauna. The ridges and hillsides above La Palma that now support scrub and pine were not long ago largely covered with broad-leaf forest. Below the frost line, pine appears to be maintained in most of the Cordillera Central by fire (of which there are many evidences, such as charred trunks) and cutting. In one place near Jarabacoa at moderate elevations, we found a hillside with many large pines, 40-50 feet tall, among which grew a dense broad-leaf undergrowth 15-20 feet tall. We could find no pine seedlings or young pine trees. It seems clear that if not disturbed, much that is now pine will be replaced by broad-leaf forest.

The present disjunct distributions of *A. christophei* and *A. etheridgei* (Thomas and Schwartz, 1967) are the results of forest destruction. Almost all of the original broad-leaf forest in which they live has now disappeared, leaving scant isolated remnants. The original distribution of this forest is mapped in the "Mapa Ecologico de la Republica Dominicana" in "Reconocimiento y Evaluacion de los Recursos naturales de la Republica Dominicana" published by the Pan American Union in 1967.

However, though today occurring only in scattered colonies, in pre-Columbian times anoles of this forest type must have been one of the dominant anole faunas of the islands, and the lowland and edge species that are now so widespread and abundant must have been restricted to very much smaller areas.

We do not know how many of the anole species that once inhabited the montane forests have become extinct during the period of dissection of these extensive forests into isolated relicts, and even among those still extant, it is certainly possible that there are still undiscovered species. (As we have mentioned above, six montane species have been described from Hispaniola in the last ten years.) Probably, however, we have a reasonably good representation of the original fauna in such small relict areas as La

Palma — at least of the "north island" portion of that montane fauna.

We do know that in these relict areas the montane species may be quite successful, and quite high population densities are sometimes reached. At La Palma we saw 35 *A. etheridgei* asleep during two hours of night collecting. (Whether this is quite as high as the densities that are reached by lowland species in some perianthropic areas we cannot be sure.)

In fact, anoles — at least some anoles — seem adapted to living in very high densities in small areas, and this is probably an important factor in their evolutionary success in the West Indies, both in persisting in relict areas and in becoming established in new ones. Anoles can live and thrive on small islands and in small patches of suitable habitat. In fact, population densities may be higher in such small areas because bird species specializing in similar habitats are absent: (such areas are too small to support them), and birds are probably the most important predators on and competitors with West Indian anoles. In the West Indies today, with its many small patches of suitable habitat (gardens, fence rows, groves of trees, little areas of forest) anoles may be generally more common than they were in earlier periods when habitats were more uniformly and continuously distributed.

Though anoles can and do survive in some very small patches of suitable habitat, they do not do so in every such spot. The advantages gained from the reduction in numbers of bird predators and competitors may sometimes be outweighed by the numbers of adjacent, potentially competing species of anoles. As at La Palma, the area around a relict forest is usually inhabited by open-country anoles with structural habitats similar to those of the forest species. As we have seen, the forest and open species generally avoid competition by occupying different climatic habitats. But in those species of anoles that have been studied in detail, some individuals do disperse into relatively unfavorable habitats and live there at least briefly. Thus at La Palma we saw occasional open-country animals within the forest. Where both open and forested areas are not too disparate in size and the population density in the open areas not too great, this invasion pressure is probably unimportant, but where one habitat is relatively much smaller than the other and the larger one is densely populated, vagrant animals from the larger population may well be an important source of competition and, in marginal cases at least, tip the balance toward local extinction of the relict population. Of course,

the smaller and more scattered the relict habitats, the more precarious this balance must be for the relict populations.

We have stressed above the abundance of anoles in certain situations, but it is important to remember that not all anoles, nor any anole species at all places and times, are abundant within their natural range. It is clearly as characteristic of West Indian anoles as of other animals that their distributions are clumped or patchy. Many of the lowland species of *Anolis* in Hispaniola or the other islands give the casual visitor the impression of overwhelming abundance. This is frequently the case in perianthropic situations, but even the commonest species are not everywhere present even in habitats that to the human eye are ideal and are continuous with areas of high population density. Rarer species may require specialized habitats that are widely disjunct, such as the rocky areas favored by *A. monticola* or *A. rimarum*. For still other species their habitat, perhaps high in the trees, e.g., *A. ricordii,* or their cryptic coloration and behavior, e.g., *A. insolitus,* reduce their visibility to the observer; for these we have no basis for an estimate of population density. We have, however, no reason not to believe that their distribution is as patchy, even within favorable habitats, as is the distribution of better known anoles. Variations in species abundance and patchiness in distribution are empirically obvious, but the factors producing them are a major unsolved ecological problem.

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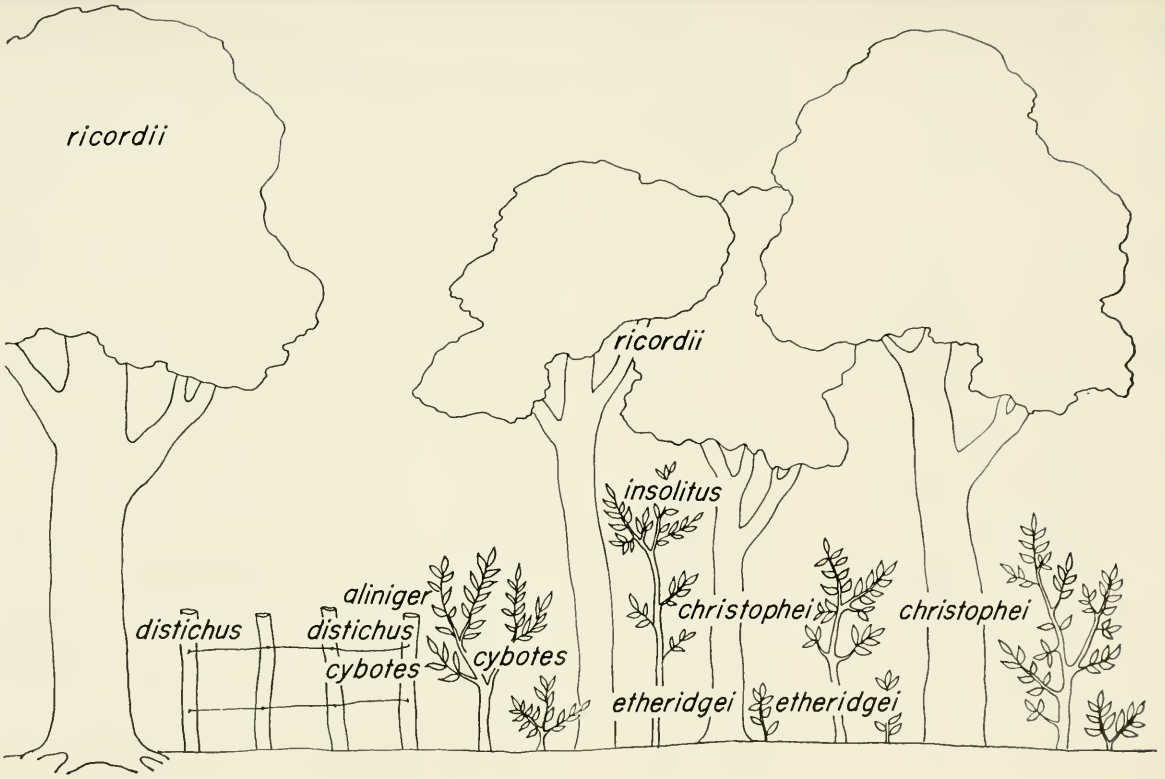

Fig. 1: Diagram of the characteristic habitats of the anoles of La Palma.

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CAMBRIDGE, MASS. 15 SEPTEMBER, 1969 NUMBER 328

A NEW FOSSIL DISCOGLOSSID FROG FROM MONTANA AND WYOMING[1]

Richard Estes

ABSTRACT. *Scotiophryne pustulosa*, n. gen., n. sp., is a small discoglossid frog from the late Cretaceous Hell Creek Formation of Montana and the late Cretaceous Lance Formation of Wyoming. It is probably also represented in the middle Paleocene Tongue River Formation of Montana. *Scotiophryne* has a distinctive pustular dermal skull, but its postcranial remains show resemblances to the Recent Eurasian discoglossid *Bombina*.

INTRODUCTION

Fossil frogs of Mesozoic age are rare; Hecht (1963) has summarized most of the occurrences. North American Mesozoic records, so far, are based on disarticulated remains, which are difficult to interpret.

Recent study of late Cretaceous and Paleocene samples of vertebrate fossils has revealed the presence of several different kinds of frogs. Lance Creek (Wyoming) and Bug Creek local faunas (Montana) are rich samples of a once widespread late Mesozoic vertebrate fauna that lived on floodplains of North American Cretaceous epicontinental seas (Estes, 1964). The Bug Creek material is from the Hell Creek Formation of Montana (Sloan and Van Valen, 1965) and is part of a Bug Creek collection in the Museum of Comparative Zoology (MCZ), Harvard University. An American Museum of Natural History (AMNH) collection from the Lance Formation of Wyoming is also utilized here. The Paleocene specimens are from Princeton University (PU) collections from the Tongue River Formation of Montana, and are part of a fauna presently being studied in collaboration with Glenn Jepsen and Marshall Lambert.

[1]Fossil Vertebrates from the Hell Creek Formation, Montana: Contribution No. 4.

ORDER SALIENTIA

Family Discoglossidae

Scotiophryne pustulosa, n. gen., n. sp.

Holotype. MCZ 3623, left ilium.

Etymology. Greek, *skotios,* dark (referring to the darkness of the fossil bones); *phryne,* toad; *pustulosa,* referring to the distinctive pustulose sculpture of the referred skull elements.

Paratypes. MCZ 3624, four left and two right ilia; MCZ 3625, 11 distal ends of humeri; MCZ 3626, 14 anterior and posterior fragments of maxillae. All specimens collected by A. D. Lewis and party.

Locality. Bug Creek Anthills, SW ¼ Section 9, T 22 N, R 43 E, McCone County, Montana.

Horizon. Hell Creek Formation, Upper Cretaceous.

Other referred specimens. AMNH 8102, right squamosal; AMNH 8132, left maxilla; AMNH 8137, right ilium; Lance Formation, Wyoming. University of California, Museum of Paleontology (UCMP) 55703, left ilium, Lance Formation, Wyoming. PU 17037, left ilium; 16784, 16827-28, humeri; Tongue River Formation, Montana.

Known distribution. Known from the Hell Creek Formation of Montana and the Lance Formation of Wyoming. A probable Paleocene record occurs in the Tongue River Formation of Montana.

Diagnosis. A discoglossid frog with ilia most similar, among modern discoglossids, to those of *Bombina,* differing from the latter in having a relatively thicker ilial shaft, slightly more expanded subacetabular expansion, and in lacking a dorsal protuberance. Differs from all recent discoglossids and most fossil forms in having a sculptured dermal skull casque. Humeri like those of *Bombina* but relatively more robust.

Description. Ilium (Fig. 1) with robust shaft having a deeply-marked groove dorsally that extends onto the dorsomedial side of the shaft, this groove well defined on the type but less strongly marked on other specimens; acetabular fossa (terminology follows Estes and Tihen, 1964) relatively large, its anteroventral border strongly produced; no dorsal protuberance as such, but dorsal prominence showing irregularities of muscle attachment; subacetabular expansion large, markedly set off from acetabular fossa and directed somewhat mediad; medially a tiny raised area on midpoint of the suture of ilium with other pelvic bones.

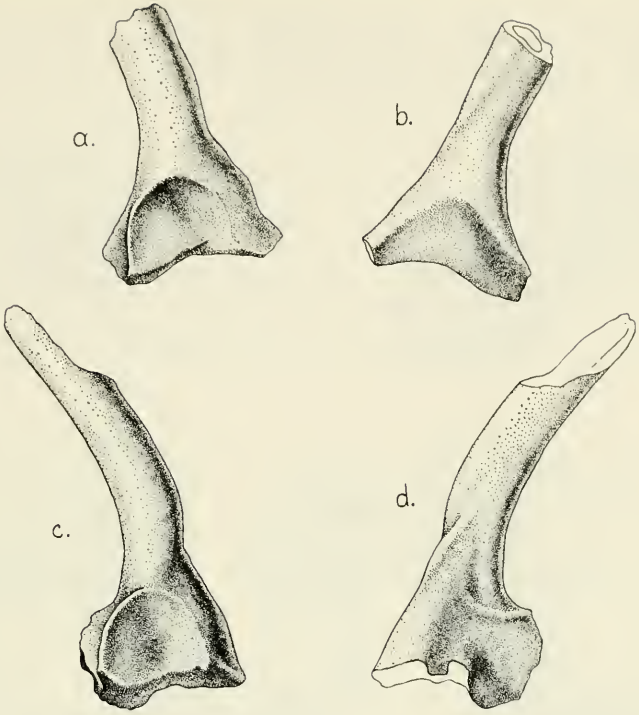

Fig. 1. *Scotiophryne pustulosa,* n. g., n. sp.: *a,* lateral, and *b,* medial views of questionably referred left ilium, AMNH 8137, loc. V5620, Lance Formation, Wyoming; *c,* lateral, and *d,* medial views of holotype left ilium, MCZ 3623, Bug Creek Anthills, Hell Creek Formation, Montana; all × 6.

Referred humeri (Fig. 3) with oblique olecranon scar (terminology as in Hecht and Estes, 1960), small but deep *fossa cubitus ventralis;* well-developed medial epicondyle and small, bi-tubercular lateral epicondyle; well-developed humeral ball, flanked by prominent lateral crest leading from shaft to proximal tubercle on lateral epicondyle, and by stronger crista medialis leading to medial epicondyle. Variable development of flattened area for muscular attachment on crista medialis probably reflects a sexually dimorphic feature not uncommon in frogs.

Maxilla (Fig. 2c-f) with broadly-expanded anterior end and prominent nasal process; posterior end expanded, pointed at its ventral tip and with notch medially for quadratojugal; dorsally an

expansion and notch for squamosal; strong pterygoid process medially; teeth numerous, small, probably pedicellate; tooth row extending posterior to pterygoid process, external surface covered with relatively fine pustular sculpture.

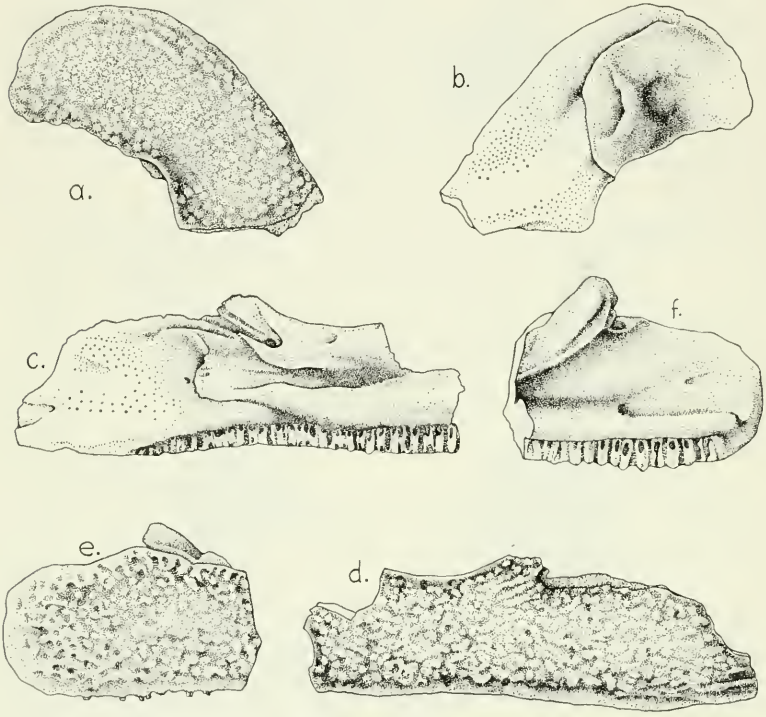

Fig. 2. *Scotioplıryne pustulosa,* n. g., n. sp.: *a,* lateral, and *b,* medial views of right squamosal, AMNH 8102; *c,* medial, and *d,* lateral views of posterior part of left maxilla; *e,* lateral, and *f,* medial views of anterior part of left maxilla, MCZ 3626; *a* - *d* from loc. V5620, Lance Formation, Wyoming; *e* - *f* from Bug Creek Anthills, Hell Creek Formation, Montana; all × 6.

Squamosal (Fig. 2a-b) compact; tympanic process expanded, rounded, with angle at ventroposterior corner; pustular sculpture as on maxillae; prominent pterygoid-paroccipital crest medially; maxillary process with medial flange.

Discussion. Ilia of discoglossids are quite distinctive, and the family reference of *Scotioplıryne* is based on the similarity of the

ilium to that of Recent Eurasian *Bombina*. The relatively large, protuberant acetabulum and weak enlargement of the iliac symphysis region also resemble the relatively better developed, similar features of the Recent Philippine genus *Barbourula* (Estes, 1964; Hecht and Hoffstetter, 1962). The humeri also show general similarity to *Bombina* in shape of ball, epicondyles, oblique olecranon scar, and dimorphism of crest development. The texture of the sculptured skull elements is distinctive, but dermal sculpture is also known in fossil discoglossids from the mid-Cenozoic of Europe (*Latonia, Zaphrissa;* Friant, 1960).

The ilium was chosen as the type specimen because it is more often recovered than the relatively more delicate skull elements.

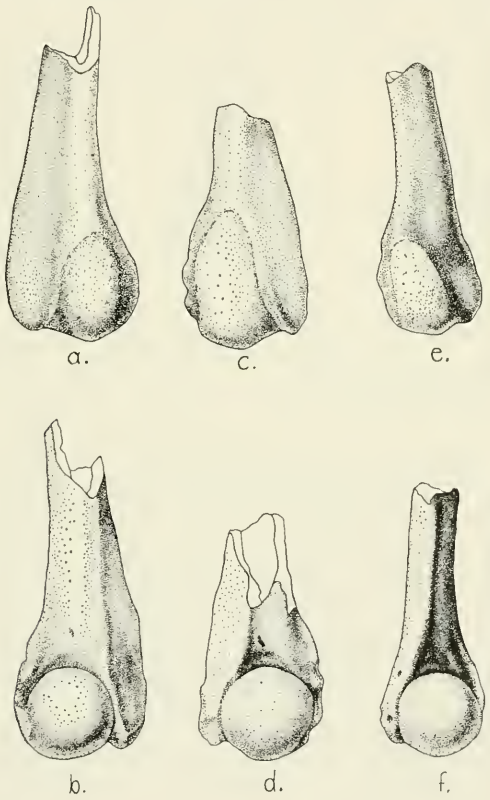

Fig. 3. *Scotiophryne pustulosa,* n. g., n. sp.: above, dorsal, and below, ventral views of distal end of three humeri, MCZ 3625; *a - b,* right; *c - f* left; *a - d* male?, *e - f* female?; all × 6; Bug Creek Anthills, Hell Creek Formation, Montana. Medial condyle of *e - f* broken, *cf.* Fig. 4 *b - c.*

The cranial, girdle, and limb parts referred to *Scotiophryne* are the most frequently-occurring frog elements in the Bug Creek sample. Three other types of frogs are also present, but are relatively rare in comparison; the *Scotiophryne* assemblage is probably a natural one based both on numerical and morphological factors.

The Princeton University specimens from the Middle Paleocene Tongue River Formation are very similar to those of *Scotiophryne,* and although worn and broken, are probably referable to this genus (Fig. 4). The other lower vertebrates from this locality closely resemble those of Bug Creek and Lance local faunas, and represent a similar flood-plain ecological association. A dimorphism (probably sexual) similar to that in the Bug Creek specimens is also shown by the Tongue River humeri.

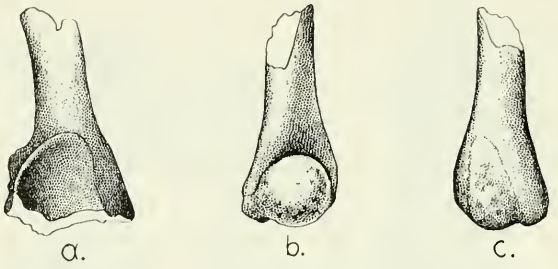

Fig. 4. *cf. Scotiophryne pustulosa: a,* lateral view of left ilium, PU 17037; *b,* ventral, and *c,* dorsal views of left humerus (female?), PU 16827; Tongue River Formation, Montana; all × 6.

Lance Formation specimens of this small, distinctive frog appear in material collected by the American Museum of Natural History and Museum of Paleontology, University of California, Berkeley. Frog remains from the Lance are more rare than from Bug Creek, but elements referred to *Scotiophryne* are also the most frequent in the Lance sample; this provides additional evidence that the association made here is the correct one. The only known squamosal referable to this species is AMNH 8102, which I figured and described as "near Leptodactylidae?" in 1964 (p. 61, fig. 32). The additional specimens described here indicate that such an identification is no longer possible. The ilium questionably referred to Ascaphidae by me (1964, p. 55, fig. 32) is probably from a small individual of *Scotiophryne.*

Scotiophryne is the second North American fossil discoglossid to be reported (the first was *cf. Barbourula,* Estes, 1964). It

resembles the Recent Eurasian discoglossid *Bombina* in some girdle and limb features, but has a distinctive sculpture of the dermal head casque. In having a broad, expanded squamosal with a tympanic process that has a ventroposterior angle, *Scotiophryne* resembles *Zaphrissa* (Friant, 1960) from the Oligocene of Germany, but the sculpture type of the latter is not pustular. The evolutionary history of *Scotiophryne* is unknown, and further comment is postponed pending more detailed studies of other fossil discoglossids.

ACKNOWLEDGMENTS

I thank Drs. Zdeněk Špinar and Max Hecht for comments. The drawings are by Mr. Laszlo Meszoly, except for Figure 4, which is by Mr. Howard Hamman. This research was supported in part by National Science Foundation Grant GB-7176.

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CAMBRIDGE, MASS. 15 SEPTEMBER, 1969 NUMBER 329

AMIA (=KINDLEIA) FRAGOSA (JORDAN), A CRETACEOUS AMIID FISH, WITH NOTES ON RELATED EUROPEAN FORMS[1]

Richard Estes and Paul Berberian

ABSTRACT. Numerous well-preserved disarticulated specimens from the late Cretaceous Hell Creek Formation of Montana show that *Kindleia fragosa* Jordan, a late Cretaceous and Paleocene amiid from North America, is referable to the Recent genus *Amia*. *A. fragosa* resembles the middle Eocene *A. gurleyi* from North America, the late Paleocene *A. russelli* from France, the middle Eocene *A. kehreri* from Germany, and the Oligocene *A. munieri* from France in a number of minor but consistent skull features. *A. kehreri* and *A. gurleyi* are relatively shorter-bodied forms than *A. calva;* the two other species were probably also short-bodied, but are known only from disarticulated or incomplete material. Most differences from *A. calva* shown by the fossil forms are minor and probably primitive. These morphological differences, and close relationship of Cretaceous seas of the western interior to the Mississippi River drainage of today, indicate that *A. fragosa* is not far from the ancestry of *A. calva*.

INTRODUCTION

Jordan (1927, p. 145) described a fossil fish from the Edmonton Formation (late Cretaceous, Alberta) as *Kindleia fragosa*, referring it to the Cichlidae. Estes (1964) demonstrated that it was an amiid, utilizing extensive material from the Lance Formation of Wyoming, and synonymized *Stylomyleodon lacus* Russell (1928) on the basis of specimens including the type bones of both described species. Russell (1968) has apparently not accepted this conclusion. Recently, Janot (1966, 1967) has described new European amiid material and has suggested that features shown

[1] Fossil vertebrates from the late Cretaceous Hell Creek Formation, Montana: Contribution No. 5.

by Lance Formation amiids indicate no more than specific distinction from *Amia*. We agree with this conclusion, which is documented below with some necessary qualifications, and *Kindleia* is here included in the synonymy of *Amia*.

Recent collections from the Hell Creek Formation of Montana (Sloan and Van Valen, 1965) have produced more material of *Amia fragosa*. This study is based on a Museum of Comparative Zoology collection made in 1964 by A.D. Lewis and party, from Bug Creek Anthills, west half of section 9, T 22 N, R 43 E, McCone County, Montana. Supplementary material from the same locality was provided by Dr. Robert Sloan (University of Minnesota). An American Museum of Natural History collection from the Lance Formation (localities V5711 and V5620: Estes, 1964; Clemens, 1963) was also utilized in this study. Almost all skeletal elements have been recovered in large numbers (except scales, in contrast with the Lance Formation collection). At least 94 individuals are represented in the MCZ Bug Creek Anthills sample.

Estes (1964) studied this species in detail, and we therefore discuss Bug Creek specimens only as they modify conclusions reached by that study. Order of discussion of bones follows that of Estes.

ORDER AMIIFORMES

Family Amiidae

Amia fragosa (Jordan, 1927)

Kindleia fragosa Jordan, 1927, p. 125
Stylomyleodon lacus Russell, 1928, p. 105

Basioccipital. Estes (1964) noted that Lance Formation basioccipitals had only one fused vertebra rather than two as in *Amia calva*. Twenty basioccipitals occur in the Bug Creek sample; nine with one fused vertebra as in the six Lance Formation specimens, and eleven with two fused vertebrae as in our six specimens of Recent *A. calva* (Fig. 2). There is a weak tendency for fusion of vertebrae to be correlated with increasing size in the Bug Creek sample; since all of our *A. calva* are approximately the same size, it is possible that such a variation exists in the Recent species as well. However, Janot (1967) has shown that variation in this feature occurs in her fossil material and suggests that it is independent of size-age variation, since even large bones may lack the additional vertebra (*ibid.*, pl. 12, fig. 2). Whatever the case, we believe that the lack of a second fused vertebra in the six Lance

Formation specimens was a chance aggregation without taxonomic significance.

The relatively short basioccipital and limited extent of the posterior brain chamber impression on it were noted for *Amia fragosa* by Estes (1964, p. 29). These features are also visible on the basioccipital figured by Janot (1967, pl. 12, fig. 6a), and differ from the widely-open brain chamber impression and somewhat longer basioccipital of *A. calva.*

Pterotic. Estes (1964) stated that a parietal lappet on the pterotic distinguished this species from *A. calva.* However, it is present in some of our *A. calva,* and the condition is also variable in the Cretaceous species. Pterotics of *A. fragosa* are consistently shorter than those of *A. calva,* and have a relatively greater anteromedial excavation for the frontal, reflecting the greater posterior extent of the latter noted below.

Parietal. The parietals lack an opening for the sensory canal. As Janot (1967) notes, this is different from the situation in *A. calva* and is a specialization of *A. fragosa.* The parietal is approximately square, rather than elongated anteriorly as in *A. calva.*

Frontal. Estes (1964) noted that orbital excavation in Lance Formation frontals was greater than in *A. calva,* and by comparison with *Sinamia* suggested the presence of supraorbitals for *A. fragosa.* Articulated specimens of *A. kehreri* (to be discussed below) from the Eocene of Europe indicate that supraorbitals are lacking in that related species, and they were probably also absent in *A. fragosa.* However, the late Cretaceous amiid *Enneles* does have supraorbitals (Silva Santos, 1960). The frontals appear to be relatively longer in *A. fragosa* than in *A. calva,* an estimated 2.8 times the length of the parietals, as opposed to 2.4 for the Recent species. This was determined in our disarticulated material by matching parts of bones of similar widths and general proportions, and by comparison with the related *A. kehreri.* The relatively long frontal and short parietal proportion is a primitive character, as judged by its presence in some other Mesozoic amioids (e.g. *Enneles, Megalurus*).

Dermosphenotic. This bone was not identified in the Lance Formation sample. Three specimens in the Bug Creek material resemble those of *A. calva* but are less elongated anteriorly, reflecting the relatively larger orbit of *A. fragosa.*

Nasal. Estes (1964) noted no difference of nasals from *A. calva.* Well-preserved Lance Formation specimens and the Bug Creek specimens all indicate a slight bifurcation of the nasal around the anterior nostril absent in our specimens of *A. calva* (Fig. 1).

Premaxilla. In 13 complete premaxillae, tooth count ranges from 6-9 teeth [frequency 6(1), 7(2), 8(9), 9(1)], as in *A. calva.*

Vomer. Number of vomerine teeth was cited by Estes (1964, p. 32) as greater than in *A. calva.* Counts based on Lance Formation and Hell Creek Formation specimens indicate a range of 18 to 24 teeth per vomer; range for the Recent species is from at

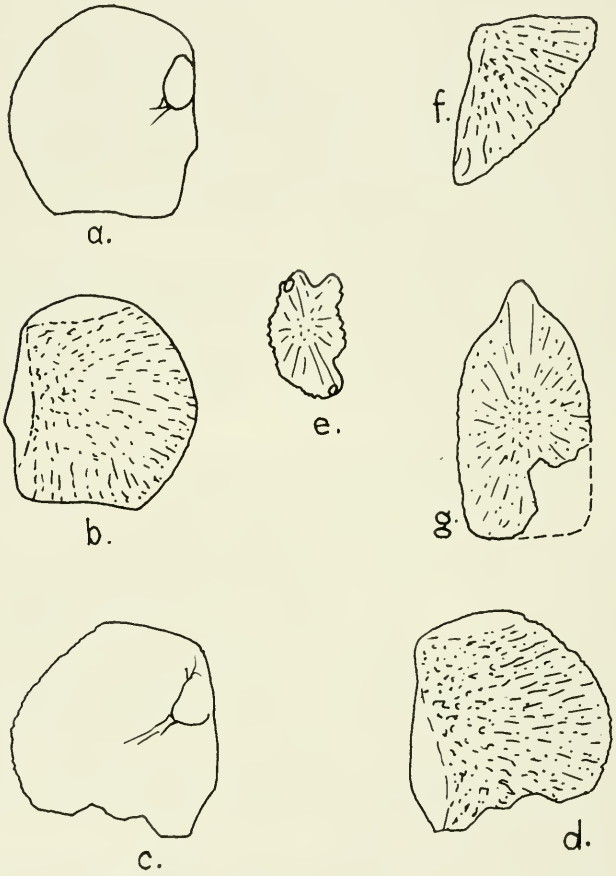

Fig. 1. *Amia fragosa: a,* medial, and *b,* lateral views of MCZ 9291, left operculum, unworn, unbroken; *c,* medial, and *d,* lateral views of AMNH 9315, left operculum, broken ventrally; *e,* dorsal view of right nasal, MCZ 9288; *f,* lateral view of MCZ 9293, left interoperculum; *g,* ventral view of MCZ 9286, gular; all × 1. AMNH 9315 from Lance Formation, Wyoming; all others from Bug Creek Anthills, Hell Creek Formation, Montana.

least 15 to 27, bracketing the fossil count. Increased vomerine tooth count must thus be removed from the diagnosis of *A. fragosa,* but the vomerine tooth patch in *A. fragosa* always extends farther posteriorly than in the Recent species, as already indicated by Estes (1964, fig. 17a, and Fig. 3b, this paper).

Dentary. As in *A. calva,* the alveolar border makes a right angle with the external face of the bone (Janot, 1967, p. 146). Few dentaries are complete enough to allow tooth count, but two have 14 and one 16 alveoli, about as in our *A. calva* sample. As in *A. russelli* Janot, coronoid attachment area is deep anteriorly in relation to depth of the jaw, and depth of jaw is greater proportionally than in *A. calva.*

Gular. This bone was not recovered in the Lance Formation material, but two gulars have been identified in the Bug Creek collection. This is a variable bone in *A. calva,* but that of *A. fragosa* is consistently shorter and less concave when compared with bones of the same width in the Recent species (Fig. 1).

Operculum. The few fragmentary opercula from the Lance sample were broken and abraded posteriorly, resulting in an inaccurate restoration by Estes (1964). The Princeton specimen thought by him to confirm the rectangular restoration given (*ibid.,* fig. 16e) is Eocene rather than Paleocene as noted (*ibid.,* p. 33), and is also broken, as more recent preparation has shown. Well-preserved Bug Creek specimens show symmetrically-rounded posterior borders with an obtuse point, similar to that of the Eocene *Amia ("Paramiatus") gurleyi* (Romer and Fryxell, 1928), *A. kehreri,* and *A. russelli.* Well-preserved Hell Creek Formation and Lance Formation specimens also confirm this shape (Fig. 1). *A. calva* usually has the blunt point in a more ventral position; the ventroposterior border of the bone in the Recent form is thus relatively more elongated. Compared with height, length of operculum is less than in *A. calva* (Fig. 3).

Suboperculum. For bones of the same anterior height, length is somewhat less than in *A. calva* (Fig. 2).

Interoperculum. The same as for suboperculum (Fig. 1).

Supracleithrum. This bone was not identified in the Lance Formation sample. A single specimen from the Bug Creek collection is more robust than that of *A. calva* and has an external surface sculptured like that of the cleithrum (as described by Janot, 1967, pl. V, fig. 4a for *A. russelli*).

Comments. The large Bug Creek sample and the American Museum of Natural History Lance Formation sample thus confirm the suggestion of Janot (1967) that *Kindleia* is a junior

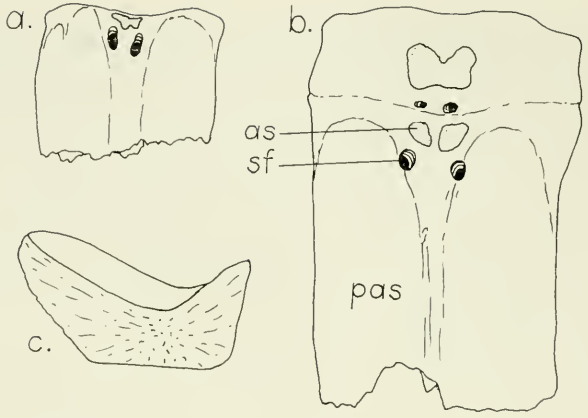

Fig. 2. *Amia fragosa*, late Cretaceous, Bug Creek Anthills, Hell Creek Formation, Montana: *a*, ventral view of MCZ 9290, basioccipital with one fused vertebra; *b*, ventral view of MCZ 9289, basioccipital with two fused vertebrae; *c*, lateral view of MCZ 9292, right suboperculum. Abbreviations: as = aortal supports, pas = parasphenoid articulation surfaces; sf = foramina for spinal arteries; all × 3.

synonym of *Amia*. Operculum shape, vomerine tooth count, and fusion of vertebrae to the basioccipital resemble conditions in Recent *Amia calva* more than was indicated by Lance Formation specimens studied by Estes (1964). However, these and other features indicate specific difference from *A. calva*. A revised species diagnosis is as follows:

1. Amiids with an estimated range of body length about the same as in Recent *A. calva*, as indicated by comparison of disarticulated elements with those of the Recent species.
2. Dermal bones about 1.5 times as thick as in *A. calva*.
3. Frontals about 2.8 times length of parietals.
4. Relatively large postorbitals, probably filling cheek region; lower postorbital much larger than upper postorbital; vertical pit line present on lower postorbital.
5. Marginal teeth simple, pointed cones, palatal teeth usually stout, styliform crushers.
6. Operculum with bluntly-pointed posterior border; opercular series relatively short anteroposteriorly.
7. Supraorbital sensory canal not entering parietal.

Related forms. Janot (1967) has agreed with Estes (1964, p. 41) that *A. munieri* of the Oligocene of France is closely related

to *A. fragosa*. Another related form is *A. kehreri* from the middle Eocene of Germany. Complete articulated specimens of this species are in the British Museum (Natural History), collected by Walter Kühne (BMNH P33480, P33488, Messel bei Darmstadt), and in the Museum für Mitteldeutsche Erdgeschichte, Halle (Saale), collected by Dr. Horst Matthes in the Geiseltal deposits (fig. 4; pl. 1). These specimens conform to the species diagnosis given above for *A. fragosa*, although the apparent absence of the supraorbital canal in the parietal cannot be confirmed without disarticulated material. In addition, they have only about 50-55 vertebral segments (counting diplospondyl centra as one pair per segment). This low number of vertebrae is also seen in *Amia ("Paramiatus") gurleyi* Romer and Fryxell (1928). *A. gurleyi* is less distinct than its describers believed, and while relatively shorter than *A. calva*, appears "deep-bodied" primarily as a result of the shorter body and of crushing. Its opercular series is very similar to that of *A. fragosa* and it has similar frontal-parietal proportions.

As noted above, *Amia russelli* Janot (1966) from the late Paleocene of France is also close to this group in several characters. The parietal Janot figures (*ibid.*, pl. IX, fig. 5) is about as wide as long, contrasting with that of *A. calva* (cf. e.g. Janot, 1967, pl. IV, fig. 6) and resembling that of *A. kehreri*, *A. munieri*, *A. gurleyi*, and *A. fragosa*. The frontal figured for *A. russelli* (Janot, pl. IX, fig. 3) is about 2.8 times as long as the figured parietal, and the latter is of about the proper size to fit the frontal. Orbital excavation in the frontal is also similar to that of *A. fragosa*. Frontal-parietal proportions of *A. russelli* thus seem to have been similar to the three species noted above. Operculum shape of *A. russelli* is generally similar to that of Cretaceous and Eocene species, being taller than wide, although the posterior angle is slightly below the middle of the bone, as in *A. calva*.

The relatively narrow proportions of the opercular series of the fossil species is a primitive character for amiids. In *A. calva* the series has widened as a result of general body elongation, although the operculum itself is always wider than or as wide as high regardless of size of the animal (Fig. 3, *c-e*).

It is thus clear that the late Cretaceous and Paleocene species discussed above are closely related, and the similarities indicate that little evidence exists for maintaining separate species *A. fragosa*, *A. russelli*, *A. gurleyi*, and *A. kehreri*. The oldest available name for the species discussed here is *A. kehreri* Andreae (1892).

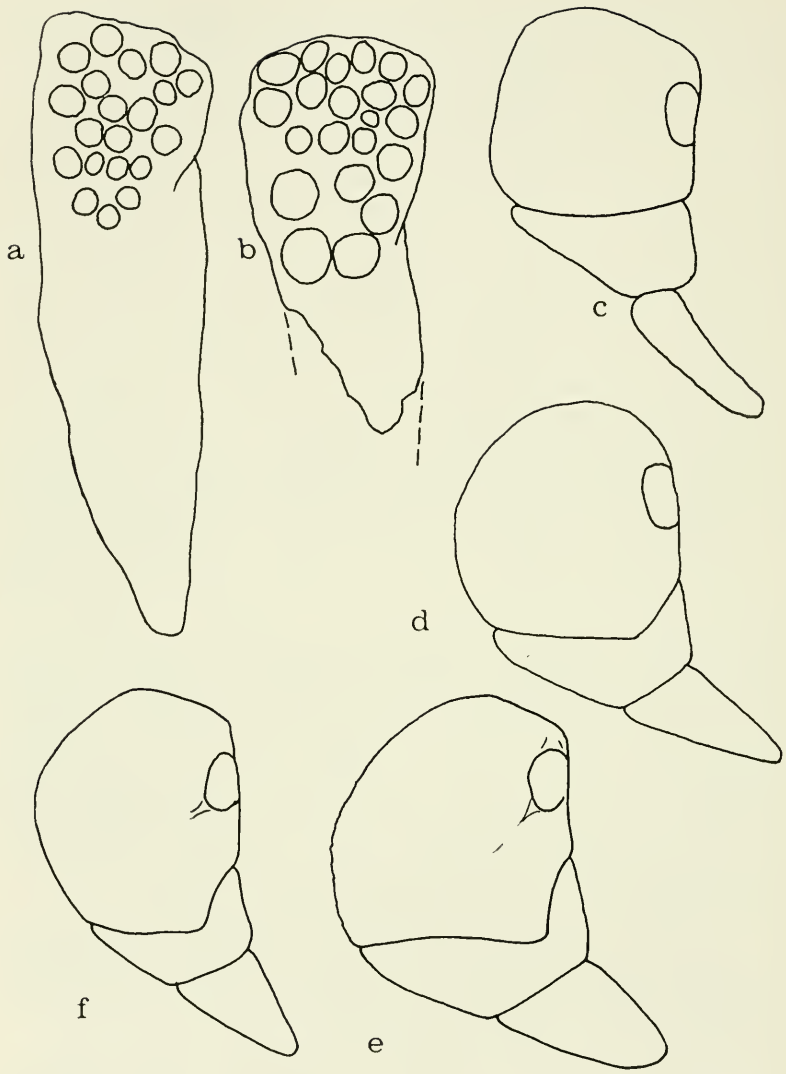

Fig. 3. *a, Amia calva*, ventral view of left vomer. *b, A. fragosa*, the same, Hell Creek Formation, Montana, MCZ 9287. *c-e, A. calva*, medial views of left opercular series; sizes: *c*, MCZ 8970, Standard Length 45 mm, *d*, MCZ 35780, SL 155 mm, *e*, unnumbered MCZ specimen, SL 425 mm. *f, A. fragosa*, restoration of opercular series. Note that in *c-e* operculum is wider than tall, whereas in *f*, Figure 4, and Plate I, it is taller than wide. *a-b*, × 3; *e-f*, × 1; *c-d* not to scale.

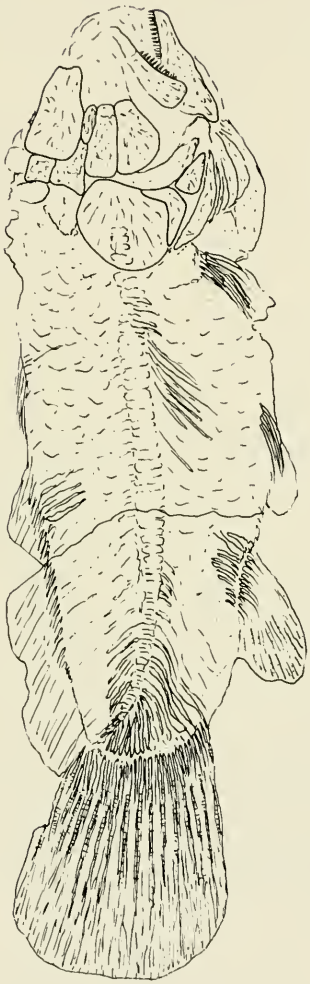

Fig. 4. *Amia kehreri*, middle Eocene, Messel bei Darmstadt. Sketch of BM (NH) P33480 made from a photograph taken by the senior author. × about ½.

We believe that *A. kehreri* and *A. fragosa* may be synonymous; temporal and geographic separation are the only known differentiating characteristics. The type of *A. kehreri* is from Messel, as are the British Museum (Natural History) specimens of this species noted above. The type is a partial skeleton, but shows the expanded lower postorbital (Andreae, 1895, pl. 1, fig. 15) more clearly seen in BMNH P33480 (Fig. 4) and the Geiseltal specimens (Pl. 1). *A. gurleyi* (Romer and Fryxell, 1928, fig. 1) also resembles *A. kehreri* in close approximation of dorsal and caudal fins, and this may be an indication that synonymy of *A. gurleyi* with *A. kehreri* is in order. Since both are middle Eocene, only geographic separation and a few minor details suggest that two species be maintained. Presence of the supraorbital canal in the parietal, somewhat larger size, and a few other superficial features seem to distinguish *A. russelli*. We do not formally synonymize any species here, however, until other early and middle Cenozoic European specimens can be studied; our purpose is merely to point out the close similarity of these Cretaceous and early Cenozoic forms (see also Estes, Hecht, and Hofstetter, 1967).

There is thus a closely related group of species of *Amia* (some probably synonymous) that is known from Cretaceous through middle Eocene of North America, and late Paleocene to at least early Oligocene of Europe. This group of species is distinct from *A. calva* only in superficial and essentially primitive ways, including relatively shorter body and skull and minor proportional differences of skull roof and mandibular bones.

The morphology of *A. fragosa* and the close relationship of North American Cretaceous seas to the Mississippi River drainage (Estes, 1964) indicate that *A. fragosa* itself cannot be far from the ancestry of the Recent bowfin. Further studies of European amiid remains, of articulated specimens of *"Protamia"* at Princeton University (Estes, 1964, p. 42), and of growth series of *A. calva* will be of considerable interest in tracing the ancestry of the modern species (see also Simpson, 1937, p. 59; specimens lost).

Stratigraphic range of Amia fragosa. Regardless of possible synonymy with European species, as noted above, the stratigraphic range of *A. fragosa* is remarkably long, extending from late Cretaceous through at least middle Eocene time in North America. No criteria exist at present for naming more than the one species. The major deposits in which remains of *A. fragosa* have been found are summarized in Table I. Unpublished records are taken from collections at the American Museum of Natural History, Princeton University, and the United States National Museum.

ACKNOWLEDGMENTS

We thank Drs. C. Janot, Charles Meszoely, and Donald Baird for data and helpful discussion. This research was supported in part by National Science Foundation Grant GB-7176, to Estes.

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(Received 8 May 1969.)

Plate I. *Amia kehreri*, middle Eocene, Geiseltal deposits. Above, skull of one individual in lateral view, showing expanded lower postorbital, opercular series, and frontal-parietal proportions; below, skull of another individual in dorsal view showing frontal-parietal proportions; × about 1.

			WYOMING	MONTANA		S. DAKOTA	CANADA
CENOZOIC	EOCENE	L					
		M	Bridger Fm., Green River Fm., Wasatch Fm.			Golden Valley Fm.	
		E					
	PALEOCENE	L		Fort Union Fm.	Melville beds		Paskapoo Fm.
		M	Rock Bench beds		Tongue River member		
		E	Mantua lentil		Tullock member		
CRETACEOUS	MAESTRICHTIAN		Lance Fm.		Hell Creek Fm.		Edmonton Fm.
	CAMPANIAN		"Mesaverde" Fm.		Judith River Fm.		Oldman Fm.

Table I. Major deposits carrying remains of *Amia fragosa* in the Western Interior of the United States and Canada. Nomenclature of units varies with author; we have therefore deliberately chosen a conservative terminology.

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THE CRANIAL EVIDENCE FOR HYBRIDIZATION IN NEW ENGLAND CANIS

Barbara Lawrence
and
William H. Bossert[1]

ABSTRACT. Using the technique of linear discrimination to compare known dog-coyote hybrids, it is shown that skulls of these animals have a mean discriminant function value almost exactly between those of the two parent stocks.

Applying this same technique to the canids which are presently invading the empty predator niche in New England, it is shown that this population differs from the known hybrids. They are predominantly coyote and evidence is given showing that they probably have some dog and wolf genes as well. The New England animals are an extreme expression of a trend already apparent in *Canis latrans thamnos* from Minnesota. The high degree of variability demonstrated is evidence that the shift away from coyoteness is the result of hybridization rather than of a rapid evolution to fit a new niche.

INTRODUCTION

Having shown (Lawrence and Bossert, 1967) that the three species of the genus *Canis: lupus, latrans,* and *familiaris,* can be clearly and significantly distinguished by the technique of linear discrimination, the question arises as to whether or not this same technique can be used to identify hybrids of these species. Part One of the present paper discusses a linear discrimination study of known *latrans* × *familiaris* hybrids; Part Two discusses the application of both this study and our earlier work to the unraveling of the ancestry of the canids that have recently been moving into the empty predator niche in New England. As in our earlier paper (1967), the measurements used for this analysis were the fifteen found to be most

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diagnostic and the technique of using the linear discriminant function to reduce the multiple measurements to a single value for each specimen was applied.

PART I
Known Hybrids

Specimens examined. Ten F_1 hybrids were measured. Five of these were from the collections of H. F. Gier at Kansas State University: two of a Labrador retriever and one of a collie crossed with two different female coyotes, two of a coyote crossed with a basenji bitch. Five more were from the collections of the University of Kansas and were offspring of a small, mongrel terrier bitch crossed with a coyote. A few additional specimens, unusuable because they were either broken or not adult, seemed by eye to fall within the range of the above.

Twelve other specimens from the Gier collection, the results of variously breeding the original hybrids amongst themselves or back to a springer spaniel, are treated separately.

Comparisons. The discriminant function values of known F_1 *latrans* × *familiaris* hybrids were calculated, on the basis of the pairwise discrimination of the two species described by Lawrence and Bossert (1967). The resulting values are intermediate between those for each species. Their range of variation is rather wider than it is for each of the parent species, but there is no overlap with either. One specimen at each end of the range is within three standard deviations of each parent form; otherwise, the F_1 hybrids cluster around a point midway between the two species. Apparently then, if the question is one of hybridization between two known species, this technique, in the majority of cases, will properly show the intermediate position of individual specimens. To what extent it would also suggest a relationship to other species was next considered.

The difference between dogs and wolves, as was shown earlier (Lawrence and Bossert, 1967), is considerably less than between any other pairs of species. For this reason, to determine how wolflike these dog-coyote hybrids are, discriminations were also tried using first the *latrans-lupus* discriminant functions and then the *familiaris-lupus*. In both instances, where only one of the paired species was actually involved in the ancestry of the hybrids, the distribution of values overlapped the values for both species used in the discrimination. While the *latrans* × *familiaris* tended to be coyotelike rather than wolflike in the first discrimination, in the

second they were more evenly distributed between dog and wolf, with the majority of the specimens actually intermediate. These relationships are shown in Figure 1.

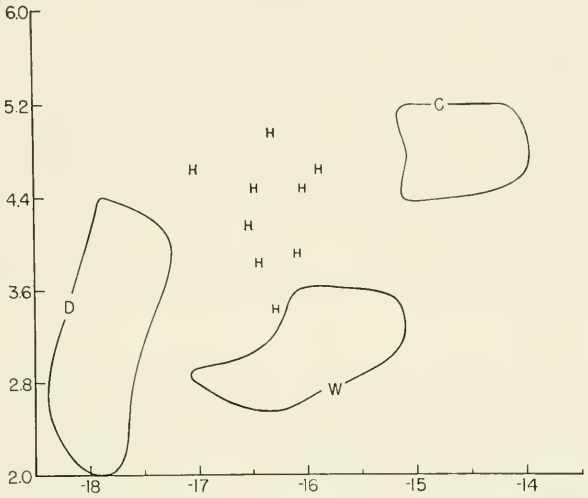

Fig. 1. Linear discriminant values of known dog-coyote hybrids (H). The *latrans-familiaris* discriminant function is used as the abscissa and the *latrans-lupus* discriminant function is used as ordinate (from Lawrence and Bossert, 1967). The contours are extreme ranges of individuals of *C. latrans* (C), *C. lupus* (W), and *C. familiaris* (D) used in computing the discriminant functions.

F_2 skulls were also studied. These were the result of subsequent crossing in various combinations, using the collie and labrador hybrids as well as a male springer. Discriminant functions were evaluated for these as for the F_1 hybrids. All fourteen proved to be intermediate between *latrans* and *familiaris* but showed a larger proportion falling within three standard deviations of one or the other. Interestingly, in the *latrans-lupus* discrimination they differ from the F_1 series in being uniformly *latrans*- like, though in the *familiaris-lupus* discrimination they coincide exactly with the F_1 series. The F_2 relationships are shown in Figure 2.

The evidence then is that, while the discriminant functions of both groups of hybrids are intermediate between those of the two parent stocks, further discrimination to see whether the trend towards dogness in particular individuals is expressed as wolfness

in a *latrans-lupus* discrimination is negative. The most doglike specimens fall within the range for *latrans* in this latter discrimination and the few specimens which are wolflike are exactly intermediate in the *latrans-familiaris* discrimination.

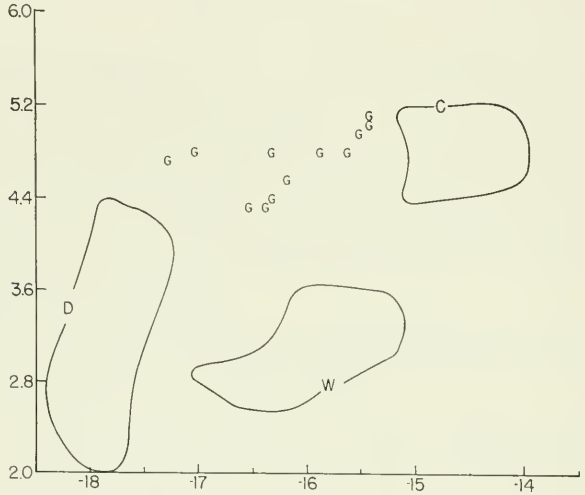

Fig. 2. Linear discriminant values of variously bred F_2 dog-coyote hybrids (G). The coordinate axes and contours are identical to those of Figure 1.

In summary, it can be said that the technique of linear discrimination can be useful for identifying hybrids between two known ancestors on the basis of multiple characters. Specimens in this category may be expected to fall between the two parent stocks. Referring specifically to *Canis,* the population of known F_1 hybrids studied is characterized by having a mean *latrans-familiaris* discriminant function value (−16.3) almost exactly between that for *latrans* (−14.6) and that for *familiaris* (−17.8). The F_2 generation is also intermediate, but the discriminant value (−16.6) tends toward that of *familiaris.*

PART II
New England Canis

Specimens examined. Twenty-two animals, offspring of siblings, dug from a den near Croydon, New Hampshire, were studied; of these, sixteen were included in the multiple character analysis. A sibling of the parents was also included, although the parents

themselves were not, as they have been kept alive for breeding. This entire series is referred to as the Boscawen series.

Of the animals collected in the wild, fifteen were suitable for inclusion in the multiple character analysis and came from the following localities: New Hampshire, Croydon, 1 male; Temple, 2 females; Lancaster, 1 male; Haverhill, 1 male. Vermont, Wardsboro, 2 females, 2 males; Brookline, 2 males. Massachusetts, Otis, 1 female; Colrain, 1 male; Leyden, 1 male, 1 female. Of these, all but the animals from Lancaster and Haverhill were typically wild in external characters. An additional fifteen specimens were either subadult or too broken for inclusion but were studied and compared with the first series. These include from New Hampshire: 2 from Croydon, 3 from Wilton, 1 from Whitefield and 3 from Colebrook, as well as six from Vermont: 1 each from Newfane, West Dummerston, Townsend, Jamaica, North Bridgewater, and Hereford.

Comparisons. Discriminant functions of skulls of the animals raised in captivity and the wild shot individuals were similarly evaluated in order to determine whether or not this population had the characteristics of the known hybrids. While the population as a whole was found to be somewhat intermediate between *latrans* and *familiaris* on the one hand, there was considerable overlap with *latrans* on the other. Even the most doglike is widely separated from *familiaris.* The mean discriminant function (−15.2) falls rather close to the range for *latrans,* and the Mahalonobis D^2 distance statistic between *latrans* and the New England animals is less than two-thirds of that between the latter and *familiaris.* On the *latrans-lupus* discrimination, the population is more completely intermediate. While the overlap with *latrans* is less, a number of specimens approach *lupus* rather closely (see Fig. 3). The average specimen is close to halfway between the two and the D^2 distances are about the same. On the *lupus-familiaris* discrimination the unknowns are again more *lupus*-like than the known hybrids. All, except one intermediate specimen, have values which fall within the range for *lupus,* whereas the known hybrids are predominantly intermediate and overlap about equally with both *familiaris* and *lupus.* These pairwise comparisons are shown in Figure 5.

The conclusions that can be drawn from these comparisons are that the unknowns differ from all three species and that they resemble coyotes more closely than the known hybrids do. They also are more wolflike. Since dogness in known coyote-dog hybrids seldom shows up as wolfness in a *latrans-lupus* discrimination, it

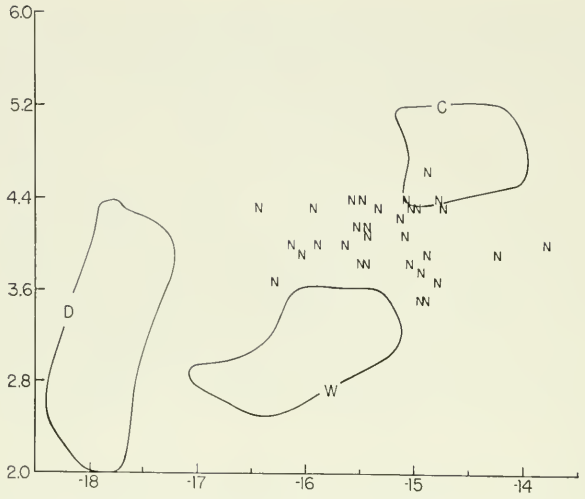

Fig. 3. Linear discriminant values of New England *Canis* (N). The coordinate axes and contours are identical to those of Figure 1.

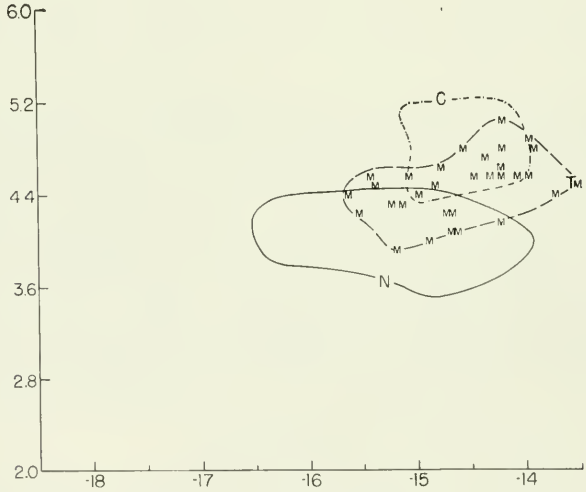

Fig. 4. Range of the linear discriminant values for *latrans* (dotted), *latrans thamnos* (dashed), and New England *Canis* (line). The coordinate axes are identical to those of Figure 1. Individual values for *latrans thamnos* specimens are shown (M).

is unlikely that the trend of the unknowns towards *lupus* can be attributed entirely to an increase of dog genes in this series.

In an effort to determine what might be responsible for the differences between the known hybrids and the unknown animals, a population of coyotes from the eastern fringe of the range of *latrans* was analyzed. Using the three pairwise discriminations described above, the discriminant functions of this series of thirty-two *C. latrans thamnos* from Minnesota were calculated and compared, not only with the original three series but also with the known hybrids and the New England population. While the Minnesota population overlaps strongly with *latrans* and has a D^2 distance

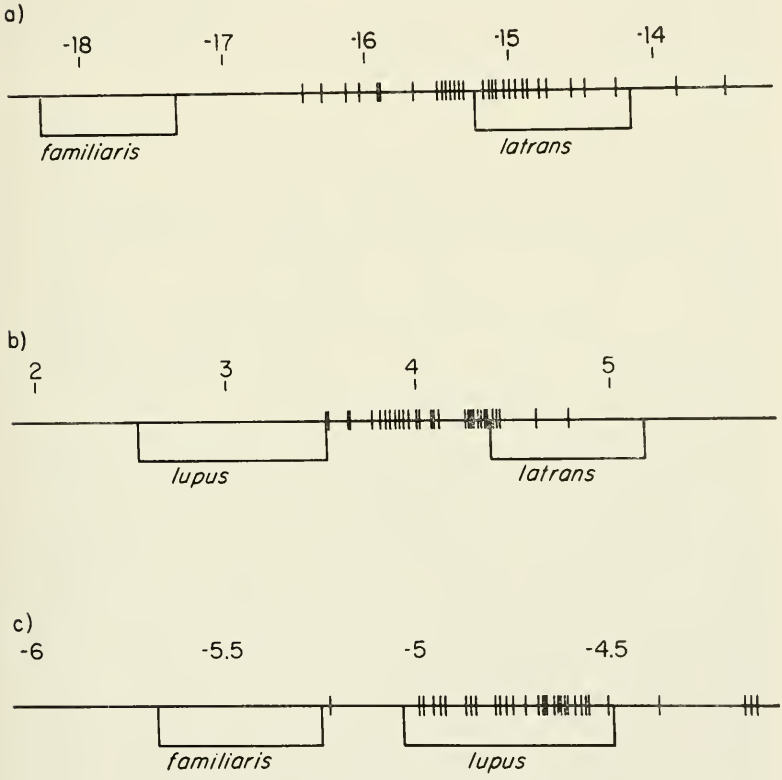

Fig. 5. One dimensional linear discriminant values of New England *Canis*: (a) on *latrans-familiaris* axis, (b) on *latrans-lupus* axis, (c) on *lupus-familiaris* axis. The range of the populations used to compute the discriminant functions are indicated by brackets.

from it that is not significant, six individuals fall well outside the range of variation as determined (Lawrence and Bossert, 1967) for the latter. Five of these are intermediate towards *lupus* in the *lupus-latrans* discrimination and only one towards *familiaris* in the *latrans-familiaris* discrimination.

Further, *thamnos* is intermediate between *latrans* and the New England population and, while it overlaps strongly with the former, it overlaps almost equally strongly with the latter, the D^2 differences between *thamnos* and each of the others being about the same. The trend away from typical coyote and towards both *lupus* and *familiaris,* already apparent in the Minnesota *thamnos*, has progressed considerably farther in the New England population, with the D^2 distance between the latter and both *lupus* and *familiaris* much reduced, and a suggestion that the trend is slightly more towards *familiaris*. The trend in the discriminant values is shown in Fig. 4.

These comparisons suggest the possibility that the divergence from the typical coyote pattern, culminating in the New England population, is, in part at least, caused by some mixing with wolf as well as with dog stocks. Further evidence is provided by the rather high degree of variability found in the two not especially isolated or reduced populations. There are several meaningful, quantitative measures of total variability in a multivariate population. We have used two that depend on the volume of the ellipsoid of variation; they are the sum of the principal axes of variation and the product of the ten largest principal axes of variation (see Cramér, 1946, p. 406). The two measures are consistent over the canid populations considered here for ranking the populations as to variability and for demonstrating relative differences in variability. These variabilities are given in Table 1. The D^2 distances between populations are given in Table 2. They show that when coyotes are compared with wolves and dogs, the within-group variation is relatively small and the between-group distances are relatively large, whereas the reverse is true when *thamnos* or the New England *Canis* are compared with wolf and dog.

In summary: although the multivariate analysis does not provide definite proof of the genetic composition of the New England population, a number of points may be deduced from it. The differences between the New England population and the known dog-coyote hybrids are sufficient to show that the former are not "coydogs." It establishes that they are, in fact, predominantly coyote, and that they are not a purely local phenomenon but are

TABLE 1

Multiple character variability within populations: Two measures of the scatter of the cranial proportions in multivariate space.

Population	Sum of principal axes of variation ($\times 10^3$)	Product of ten largest axes of variation ($\times 10^{42}$)
C. familiaris	3.40	13.5
C. lupus	1.00	0.14
C. latrans	0.66	0.02
C. latrans thamnos	1.28	1.42
New England *Canis*	1.69	8.22

TABLE 2

Mahalonobis D^2 distance statistics between populations.

	C. familiaris			
C. lupus	27.2	*C. lupus*		
C. latrans	119.9	64.1	*C. latrans*	
C. latrans thamnos	—	—	6.71	*C. latrans thamnos*
New England Canis	44.55	29.84	26.83	9.12

extreme examples of a progressive change that had already begun on the eastern periphery of the coyote's distribution.

Discussion. In external appearance, the specimens under consideration are not unlike large coyotes. They have agouti hair, and the rather common, wild-canid color pattern found in varying degrees of intensity in all coyotes, in some wolves, and approximated in some dogs. The tail is carried straight, not curled up at the tip, and has the rather bottle-brush appearance characteristic of both coyotes and wolves and quite distinct from that of dogs. The ears are always erect, and vocalization and smell are undoglike (Silver and Silver, in press). On the grounds of external appearance alone, it might seem a justifiable assumption that the New England animals are examples of a rapid evolution of a race of coyotes characterized by large size and more powerful teeth suited to preying on large mammals.

The multiple character analysis, which shows a definite trend away from coyote towards both dog and wolf, slight in the Minnesota animals and more extreme in the New England population, could also be interpreted this way. Such a composite picture of the characters, however, masks the extent to which usually diagnostic features of different species may be developed in the same individual. These combinations of non-homogeneous characters strongly suggest multiple ancestry.

In considering cranial variations, it is important to keep in mind that the animals raised in captivity in Boscawen, offspring of a single pair of adults, have a common genetic background while the wild shot individuals come from a scattered, spottily distributed population which may be anything but homogeneous.

Individual skulls of the Boscawen series (F_1 litters) vary from coyotelike (cf. MCZ 51726, 27) to ones which are coyotelike in narrowness of rostrum, shape of brain case and interorbital region, but are uncoyotelike (cf. MCZ 51865, 66) in their widely spreading zygomatic arches, reduced bullae, shortened rostrum, and somewhat elevated forehead with a well-developed frontal concavity between the broadly spreading frontal processes. Most agree in having length of jaw incompatible with size of teeth and, in many, the premolars actually overlap. All have M2/well developed as in coyotes and, in general, the cusps of the molars are rather blunt and rounded as in dog/wolf. Otherwise, variation in P/4 and M/1 and in P4/ and C/ spans the range between coyote and dog/wolf.

The wild shot specimens examined, setting aside those that on the basis of external characters were at least part dog, are similarly heterogeneous. Some have a broad brain case and zygomatic arches, combined with a narrow rostrum. A number have the premolars crowded and overlapping but none have the rostrum as shortened, relative to the size of the teeth, as do some of the Boscawen series. In addition, a given tooth row often combines, interestingly, coyote with wolf/dog characters. The most coyotelike of the characters are the rather uniformly large inner portion of M1/ and the large size of M2/. These are combined with short, broad canines, a reduction of the metaconid of M/1, upper carnassials that tend towards wolf/dog not only in plumpness but also in the slight development of the deuterocone, and an overall massiveness of the teeth in relation to size of skull.

The most conspicuous and possibly significant variation is in the size of these wild shot animals. The most wolflike one and one of the most coyotelike, as shown by the multiple character analysis, are also at opposite extremes in total size and, more particularly,

in size of teeth. Both specimens were shot in Leyden, Massachusetts, and apparently belonged to the same small pack.

In the series as a whole, the largest skulls are at the upper extreme of reported size for coyotes and in certain dimensions, notably zygomatic width and width across condyles, are actually larger than reported coyotes, (Young & Jackson, 1951). These specimens often resemble closely skulls of some of the southern, probably hybrid, animals sometimes called *Canis niger gregoryi*. They are almost equally close in size and general appearance to small specimens of the northern timber wolf, *Canis lupus lycaon,* on whose range they have begun to impinge. The same is true of certain tooth dimensions; extreme individuals have a massive upper carnassial with a breadth to length ratio that falls outside of the range for coyotes; even more conspicuous is the greater width of the often shortened canine. These largest teeth again approach certain of the specimens referred to above of so-called *niger gregoryi* and are close to those of some of the smallest wolves. Such big teeth are not, however, necessarily associated with the biggest skulls.

The similarities between both the wild shot and the Boscawen animals support the theory that the two are closely related. The multiple character analysis shows this total population to have certain characteristics in common and, further, to differ more from the known hybrids than it does from the Minnesota population. That this is not evidence of rapid evolution of pure coyote stock to suit the prey and habitat requirements of the Northeast is suggested by the extreme and uncoyotelike combinations of certain characters described above as well as by the high degree of variability discussed earlier. Further, it seems that some of the traits found, such as the slender rostrum and crowded teeth, would have no selective advantage for an animal preying on large game. Finally, some of the unmeasurable characters usually diagnostic for dog/wolf, such as reduction of the metaconid of M/1 and shape of the postorbital region, or for dog such as flattened bullae, suggest some heterogeneity. Probably what has occurred is that animals of mixed but predominantly coyote ancestry have survived and bred amongst themselves, adapting rather easily, as *Canis* does, to shifting environmental conditions as they have moved east. The differences between these animals and the known hybrids, their intermediate position when compared with *lupus,* and the rather large size, especially of teeth, all suggest further that wolf as well as domestic dog is involved in their ancestry.

Although studies have not been made in detail of animals from areas between New England and the erstwhile extreme eastern edge of the range of *latrans thamnos*, individual specimens from the Adirondacks and the St. Lawrence Valley, as well as reports of difficult-to-identify *Canis* from southern Ontario, all suggest that we are dealing with a rather widespread phenomenon, which very likely parallels that found in the southern states where, along the eastern edge of the coyotes' extending range, "red wolves" are reported. That these animals are not a distinct species and the possibility of hybridization were discussed in our earlier paper (1967: 230). While there is considerable resemblance between individual specimens from the different areas, the New England population on the whole seems less wolflike, though both populations agree in being highly variable.

SUMMARY

Cranial studies of the population of *Canis,* which is presently expanding into the empty predator niche in New England show that these animals are predominantly coyote and probably have some dog/wolf ancestry. A multiple character analysis shows that they differ from known dog-coyote hybrids, which are intermediate between the two parent stocks. The New England animals are closely related to *C. latrans thamnos,* a Minnesota population that has already begun to move away from typical *latrans* towards both *familiaris* and *lupus.* That these changes cannot be entirely accounted for as evidences of a rapid evolution of coyote stock is shown by the high degree of variability of the population, the nonhomogeneous combinations of certain features, and the possession of some particular characters usually considered to be diagnostic for dog/wolf. The differences, as shown by the multivariate analysis, between this population and that of known dog-coyote hybrids further suggest that wolf as well as dog genes have been introduced. The conclusions arrived at in these cranial studies are in agreement with the behavioral trends noted by the Silvers (in press).

Because of our present imperfect knowledge of these animals, their probable hybrid ancestry, and undiagnostically wide variation of cranial characters, no trinomial is proposed for them; rather they should be called *Canis latrans* var. and may be referred to as the eastern coyote.

ACKNOWLEDGMENTS

This work is part of a joint study of New England *Canis* undertaken in cooperation with Helenette and Walter T. Silver of the New Hampshire State Fish and Game Department. Their work on comparative behavior of these animals is in press (Wildlife Monographs). The Boscawen animals used were raised by them, and the authors are indebted to them for also supplying most of the wild shot specimens. We are grateful as well to the many individuals who collected these.

The authors are much obliged to Dr. H. T. Gier of Kansas State University for his kindness in allowing us to study his excellent series of dog-coyote hybrid skulls, and to Drs. J. Knox Jones, Jr. and Robert M. Mengel of the Museum of Natural History, University of Kansas, for the loan of additional hybrid material. Our thanks also go to Dr. W. M. Breckenridge of the Minnesota Museum of Natural History for the series of *C. l. thamnos,* to the Illinois State Natural History Survey, the United States National Museum, and the Ministère de la Chasse, Faune Terrestre of the Province of Quebec for supplementary specimens.

This work has been supported primarily by National Science Foundation grant GB-1265 and also by the Department of Biology and the Milton Fund of Harvard University.

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(Received 8 May 1969)

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Museum of Comparative Zoology

CAMBRIDGE, MASS. 24 OCTOBER, 1969 NUMBER 331

A SCINCOID LIZARD FROM THE CRETACEOUS AND PALEOCENE OF MONTANA[1]

Richard Estes

ABSTRACT. *Contogenys sloani*, n. gen., n. sp., is a scincoid lizard from the late Cretaceous Hell Creek Formation and middle Paleocene Tongue River Formation of Montana. Its closest relationships seem to be with primitive members of the Scincidae, and it is tentatively referred to that family. *Contogenys* is specialized in possession of short mandibles with the posterior teeth diminishing little in size relative to anterior ones.

INTRODUCTION

Hoffstetter (1962), in describing known finds of fossil Scincidae, cited a late Cretaceous record (later described as *Sauriscus;* Estes, 1964), and noted that no other North American scincid fossils were known before the late Pliocene. In 1963 I described an early or middle Miocene occurrence of *Eumeces* from Florida, in 1964 Estes and Tihen noted a probable occurrence of *Eumeces* in the late Miocene or early Pliocene of Nebraska, and in 1965, I reidentified as *Eumeces* a middle Oligocene skull from Nebraska. A second middle Oligocene skull of *Eumeces* is now known from North Dakota (Frick Collection, American Museum of Natural History, FAM 42916). The Cenozoic record of Scincidae in North America is therefore now much better documented than it was at the time Hoffstetter's review was written.

Sauriscus, from the late Cretaceous of Wyoming, was referred to the Scincidae on the rather tenuous grounds that it possessed a prominent, upturned coronoid process of the dentary (Estes, 1964). Admittedly, while it may be a scincid, *Sauriscus* is known only from dentaries and maxillae, making it difficult to distinguish from the related Cordylidae and Gerrhosauridae on other than zoogeographic grounds.

[1] Fossil vertebrates from the Hell Creek Formation, Montana: Contribution No. 6.

The presence of still another scincid-like form in the late Cretaceous Hell Creek Formation of Montana is therefore of considerable interest. As with the Lance Formation specimens, the Hell Creek fossils are disarticulated, but a fragmentary dentary from the middle Paleocene of Montana, with postdentary bones in articulation, allows comparisons with other families to be made with somewhat greater assurance.

ORDER SAURIA

SUBORDER SCINCOMORPHA

Superfamily Scincoidea

Family Scincidae?

Contogenys sloani, n. gen., n. sp.

Type. MCZ 3681, almost complete left dentary.

Paratypes. MCZ 3682, fragmentary right maxilla; 3683, fragmentary left dentary; 3684, twelve fragments of dentaries; 3685, two parietals. Collected by A. D. Lewis and party, 1964.

Type locality. Bug Creek Anthills, Hell Creek Formation, SW ¼ Section 9, T 22 N, R 43 E, McCone County, Montana.

Age. Late Cretaceous.

Etymology. Greek, *kontos,* short; *genys,* jaw. The specific name is for Dr. Robert E. Sloan, who has done most of the collecting in the Bug Creek area.

Referred Specimens. Princeton University (PU) 17035, right dentary; 17036a, broken left dentary; 17036b, posterior end of right dentary with associated coronoid, splenial, and parts of surangular and angular. Tongue River Formation, Medicine Rocks, T 3 N, R 58 E, near Ekalaka, Carter County, Montana; middle Paleocene.

Diagnosis. A short-jawed scincoid lizard; a prominent labial coronoid process of dentary present; deep lingual coronoid notch occurring on dentary, posterior to tooth row; blunt, homodont teeth with squared-off crowns that have faint anterior and posterior crests; 13-15 dentary teeth; posterior dentary and maxillary teeth diminishing very little in size and height.

Description. The dentary is relatively short and blunt, and the Meckelian groove is narrowly open to the symphysis. Dorsoposteriorly the dentary turns sharply upward at its tip, forming a small but prominent coronoid process. The posterior edge of the dentary curves ventrally and then turns sharply caudad, forming a prominent ventroposterior (or Meckelian) process, the tip of which is

broken off in the Cretaceous specimens but is present in the Paleocene specimen PU 17035. The external surface of the dentary is smooth and has a row of mental foramina; a depressed channel is present near the parapet of the jaw, ventral to the teeth. Labially, between coronoid process and ventroposterior process, there is a distinct depression for attachment of the adductor musculature. Lingually a deep facet for the coronoid is impressed on the dentary, just posterior to the tooth row. There are thirteen teeth in the complete tooth row preserved on the type, although all but four of the teeth are broken. The tooth row ends posteriorly without marked reduction in tooth size. There may have been an additional tooth on the now missing anterior tip. The teeth are strongly pleurodont and are bordered lingually by a deep, well-defined *sulcus dentalis*. The vertical tooth shafts are regularly spaced; they are quite slender and closely spaced anteriorly, increasing in diameter and in spacing posteriorly. They project about a third of their total height above the external parapet of the jaw. The tooth crowns are blunt, slightly compressed linguolabially, and are essentially smooth on both lingual and labial sides. Faint vertical anterior and posterior crests are present in the lingual side of the crowns (Fig. 1). PU 17035, a right dentary, resembles the Cretaceous specimens in every way (Fig. 4).

The maxilla is expanded posterolaterally and a triangular wedge protrudes posterodorsally, which evidently inserted into the jugal. The tooth row ends abruptly without marked reduction in size or height of posterior teeth (Fig. 2).

The referred parietals are short, with widely-divergent supratemporal processes. Dorsally, they have a rather coarse, rugose osteoscutal sculpture. The interparietal scale impression is prominent and raised, but no other epidermal scale markings are present. The parietal foramen is well developed. Ventrally, temporal muscle areas are present on each side, but they do not extend onto the dorsal surface of the bone. A postfrontal or postorbital facet is present anterolaterally. Posteroventrally, a deep pit for the parietal ligament is flanked by prominent supraoccipital attachment areas (Fig. 3).

PU 17036b, a specimen from the middle Paleocene Tongue River Formation of Montana, shows that the splenial is large and fills the Meckelian groove, extending posteriorly under the coronoid, and indicates the nature of the labial sutures and processes of dentary and postdentary bones. There is a tongue-like process of the coronoid separating coronoid process of the dentary from the anterior surangular foramen (Fig. 5). The latter lies entirely on the

surangular. Lingually the angular reaches anteriorly to about the midpoint of the surangular "window", and the relatively large splenial has a large anterior and small posterior mental foramen, both placed rather far posteriorly.

Discussion. The following combination of characters suggests that *Contogenys* is closely related to the scincomorph superfamilies Scincoidea and Cordyloidea: (1) tooth crowns with weak ridges on anterior and posterior edges of the lingual side; (2) strongly divergent posteroventral and coronoid processes of the dentary; (3) labial coronoid process of the dentary that laps up onto the anterior edge of the coronoid bone; and (4) prominent labial tonguelike projection of the coronoid behind coronoid process of dentary. All Lacertoidea (Teiidae and Lacertidae) have a strong anterior process of the coronoid overlapping the dentary, unlike scincoids, cordyloids and *Contogenys* (Fig. 5).

In labial view, the surangular and angular do not extend anteriorly beyond the most posterior tooth, thus resembling the scincids but differing from the cordyloid condition (Fig. 5). The wedge-shaped, laterally-projecting posterior border of the maxilla of *Contogenys* resembles the condition in many Scincidae, especially Scincinae such as *Eumeces,* in which this wedge fits into a notch in the jugal. Greer (1969) has placed the Scincinae as the most primitive of the scincid subfamilies.

The laterally-crested, blunt teeth of *Contogenys* resemble those of primitive scincids and gerrhosaurids, although they lack the lingual striations commonly present in the latter two groups. Cordylids and the Lacertoidea usually have bi- or tricuspid teeth and relatively long, slender dentaries, unlike *Contogenys.*

The late Cretaceous *Sauriscus* (see p. 1) has a long, slender jaw, bifid teeth, and extension of the notch for surangular and angular anterior to the termination of the tooth row; in these features it resembles the Cordyloidea more than the Scincoidea, and future finds may necessitate its removal from the Scincidae. In any case, there is no resemblance to *Contogenys.*

The posterior end of the tooth row of *Contogenys* appears abruptly truncated because of unreduced size of the posterior teeth. The microteiid *Neusticurus ecpleopus* resembles *Contogenys* in this adaptation, but differs significantly in tooth type, closed Meckelian groove, long labial dentary process of the coronoid, and other features. Adaptation to a particular diet may have produced a similar arrangement in the two species, which are certainly unrelated.

The parietals of *Contogenys* superficially resemble those of primitive Scincinae in having a raised interparietal scute area and in apparently having an open upper temporal fenestra. The anteroposterior shortness of the bone is a resemblance to the Lacertidae and to some cordyloids, although it can be matched in some scincids. The ventral epipterygoid flanges of the parietal that occur in Scincidae are absent in *Contogenys*.

Scincoidea and Cordyloidea are probably more closely related to each other than they are to Lacertoidea (Hoffstetter, 1962), and it is to be expected that ancient members of these families (as well as modern ones, so far as dentary structures are concerned) would be difficult to discriminate. Tentatively, I refer *Contogenys* to the Scincidae on the basis of the *Eumeces*-like wedge on the posterior border of the maxilla and on the general appearance of the teeth. If the parietals are properly referred, the open upper temporal fenestra could also be included as a scincid resemblance, although this primitive condition is also present in the Jurassic cordyloid *Paramacellodus* (Hoffstetter, 1967). On the other hand, absence of the characteristic ventral (epipterygoid) flanges of the parietal found in all living scincids casts doubt on the reference to Scincidae. However, lacking more assurance of the association of the parietals, even a questionable reference to the Scincidae is preferable on both morphological and zoogeographical grounds than is a suggestion of relationship to cordyloids.

ACKNOWLEDGEMENTS

I thank Allen Greer for helpful comments. Figures 1a and 2a were prepared by Miss Tehrie Holden, figures 1b, 2b and 3 by Laszlo Meszoly, figure 4 by Howard Hamman. This research was supported in part by National Science Foundation Grant GB-7176.

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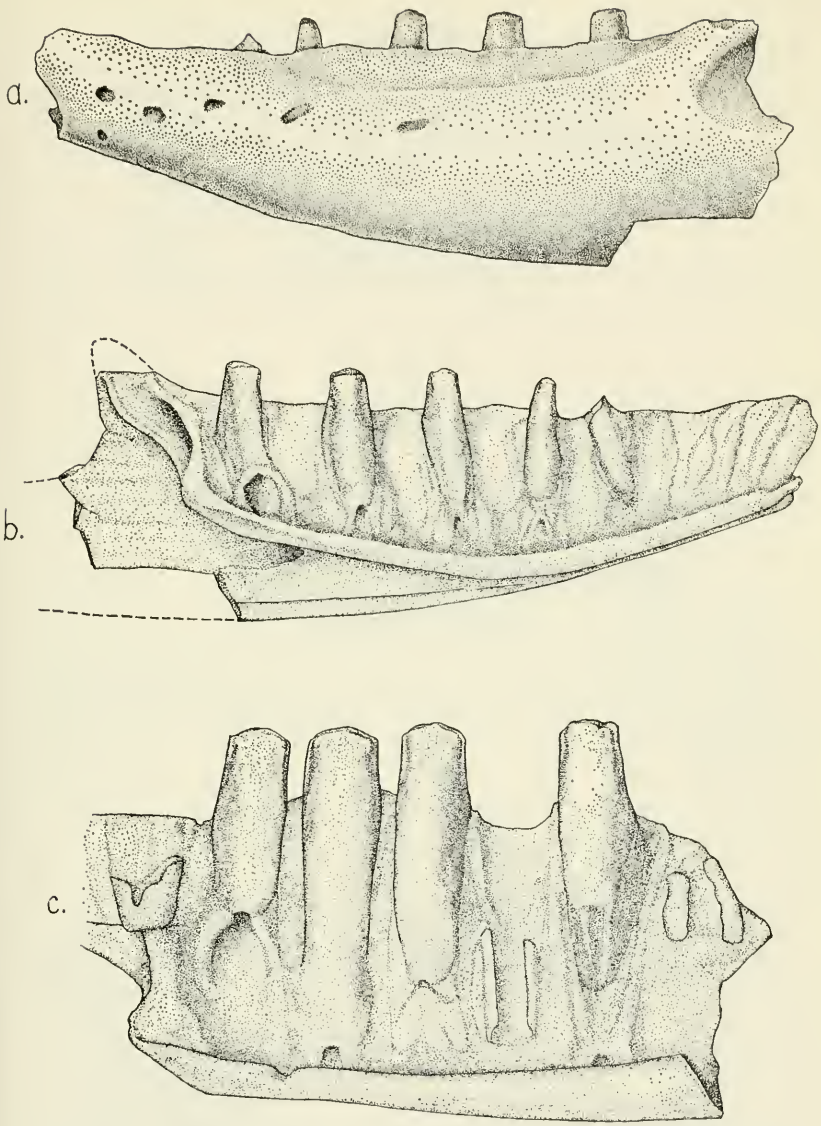

Fig. 1. *Contogenys sloani, a,* MCZ 3681, type left dentary, labial view, restorations made from other specimens; *b,* the same, lingual view; *c,* MCZ 3683, detail of four teeth from fragmentary left dentary, lingual view. *a-b* × 13; *c* × 27; Hell Creek Formation, Montana, late Cretaceous.

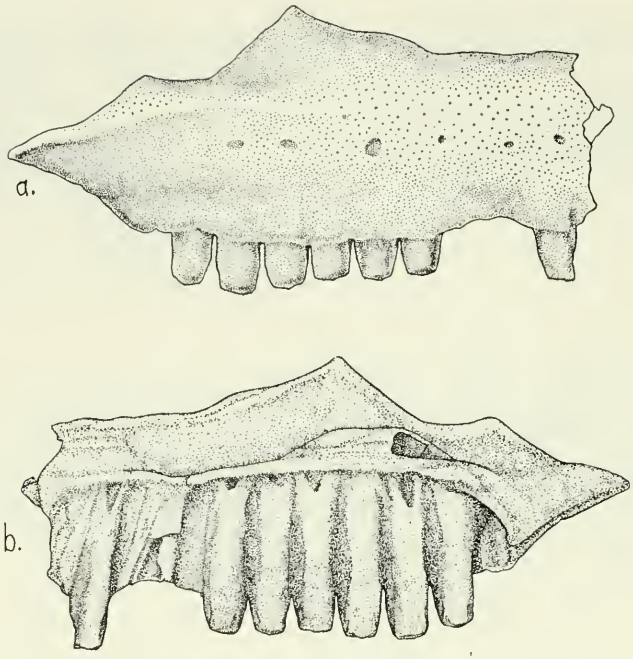

Fig. 2. *Contogenys sloani,* MCZ 3682, posterior portion of right maxilla; *a,* labial, *b,* lingual view; × 13; Hell Creek Formation, Montana, late Cretaceous.

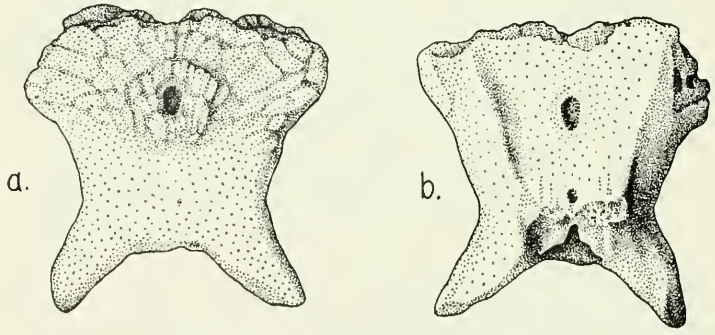

Fig. 3. *Contogenys sloani,* MCZ 3685, referred parietal. *a,* dorsal; *b,* ventral view; × 5; Hell Creek Formation, Montana, late Cretaceous.

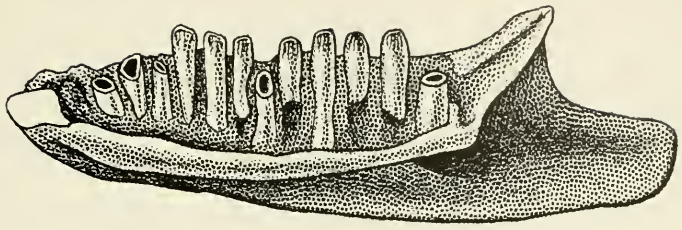

Fig. 4. *Contogenys sloani,* PU 17035, right dentary, lingual view; × 10; Tongue River Formation, Montana; middle Paleocene.

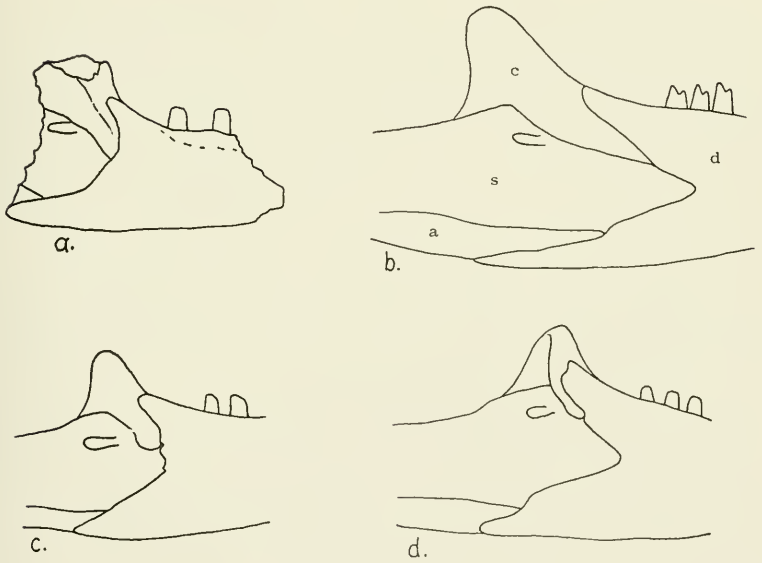

Fig. 5. Patterns of labial dentary-postdentary bone articulation in right mandibles of various lizards. *a, Contogenys sloani,* PU 17036b, Tongue River Formation, Montana, middle Paleocene; *b, Gerrhosaurus flavigularis,* MCZ 50988; *c, Eumeces longirostris,* MCZ 20508; *d, Cordylus cordylus,* MCZ 21570; all × 6.5. Abbreviations: a=angular, c=coronoid, d=dentary, s=surangular.

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Museum of Comparative Zoology

CAMBRIDGE, MASS. 24 OCTOBER, 1969 NUMBER 332

THE BRAZILIAN TRIASSIC CYNODONT REPTILES *BELESODON AND CHINIQUODON*

Alfred Sherwood Romer

ABSTRACT. Skulls of the carnivorous cynodonts *Belesodon* and *Chiniquodon* from the Triassic Santa Maria beds of Brazil are described and figured, as well as mandibles and postcranial materials of the latter genus.

INTRODUCTION

In connection with current studies on the cranial anatomy of carnivorous cynodonts from the Triassic Chañares Formation of Argentina, my attention has been recalled to two apparently related cynodonts, *Belesodon* and *Chiniquodon*, from the Middle Triassic Santa Maria Formation of Brazil. These forms were described by Huene (1944), but described on such imperfect cranial material that their relationships and much of their structure have remained in doubt.

Only a single specimen of each was present in Huene's collection. Of *Belesodon*, the skull was nearly complete, but somewhat distorted and obviously rather crushed, so that Huene, although figuring it in dorsal and ventral aspects, was unable to give satisfactory lateral views. Further, its cheek teeth had been lost, so that it was even suspected at one time of being a gomphodont rather than a carnivore (Bonaparte, 1963). Of *Chiniquodon*, only a fragmentary and battered skull was found, and although a carnivorous dentition was partially preserved, little of cranial structure can be made out from Huene's published photographs. Bonaparte (1966) has described a specimen from the Ischigualasto beds (later in time than those of Santa Maria), which he believes to be a surviving *Chiniquodon*, but this specimen is likewise very fragmentary in nature.

For the two genera, Huene established the family Chiniquodontidae in 1956, but he gave no diagnosis of this new group; indeed, few facts were available which could be utilized for a family

definition. However, comparison with obviously similar specimens from the Chañares Formation has helped to clarify the nature of the Santa Maria forms, as have notes given me by Sr. Bonaparte resulting from a recent study of Huene's specimens. The general nature of the two genera is now clear. *Belesodon* possessed, it is certain, a dentition similar to that of *Chiniquodon,* and the two are closely related.

A major aid to understanding comes from undescribed materials[1] in the Museum of Comparative Zoology, collected by a Brazilian expedition in 1936, conducted by Dr. T. E. White and

Fig. 1. Dorsal view of the *Belesodon* skull, MCZ 1533, as preserved. × ⅓.

[1] Preparation of the material here described was made possible by National Science Foundation Grant GB-500.

L. I. Price, in the Santa Maria beds. These include a skull (MCZ 1533) comparable to Huene's *Belesodon* type, and two skulls which appear referable to *Chiniquodon* (MCZ 3614, 3615). These skulls were collected south of Candelária, State of Río Grande do Sul, in Santa Maria beds apparently comparable to those in which Huene had collected at Chiniquá. In this area, the Harvard expedition collected a considerable quantity of dicynodonts, a few cynodonts, and a single archosaur. As at Chiniquá, and in contrast to the Santa Maria area, no rhynchosaurs were found. Price has later collected more material from this region, including the only South American procolophonid (Price, 1947), and collaborated with E. H. Colbert in collecting still further Candelária specimens for the American Museum of Natural History.

The skull specimens described here are somewhat distorted, and furthermore, as in much Santa Maria material, action subsequent to burial (probably thermal, perhaps due to the superposed Serra Geral volcanics) has resulted in the presence of numerous breaks of the bone surface, giving an effect similar to that of "crackleware" pottery (Fig. 1). This has made it difficult to be sure of the sutural pattern in many instances. In my figures, I have to some degree "idealized" the specimens, correcting dislocations and distortions, omitting obviously unnatural breaks and cracks, and filling in the outlines of various minor deficiencies. This may have resulted in minor inaccuracies, but I do not believe them serious, and this procedure yields a better understanding of skull morphology than would a literal portrayal of damaged detail. Since I am elsewhere describing much better preserved Chañares relatives, I shall give here only a very general account of the Santa Maria material.

BELESODON

(Figs. 1-5)

The MCZ *Belesodon* skull (No. 1533) measures 224 mm in length from premaxilla to occipital condyles. It is thus rather comparable in size to Huene's type, in which this same measurement is 258 mm. The general skull proportions (and those of *Chiniquodon* as well) are similar to those of the earlier (and more primitive) cynodonts of the family Thrinaxodontidae. The center of the orbit is slightly anterior to the mid-length of the skull, whereas in the type, as figured, it is very slightly posterior. Septomaxillae are present, but somewhat displaced, and their posterior limits are not clear; presumably they conformed to the usual cynodont pattern.

The orbital rim is imperfect in the lacrimal region, but there does not seem to have been development of the somewhat variable protuberances seen in other chiniquodontids, along the rim anterior to the lacrimal duct. Anterior to this point, on the boundary between lacrimal and maxilla, there is a well-marked pit which appears not to have been present in the *Belesodon* type. The sagittal crest is high, and the two parietals are closely appressed, although not fused. There is a narrow cleft between the parietals

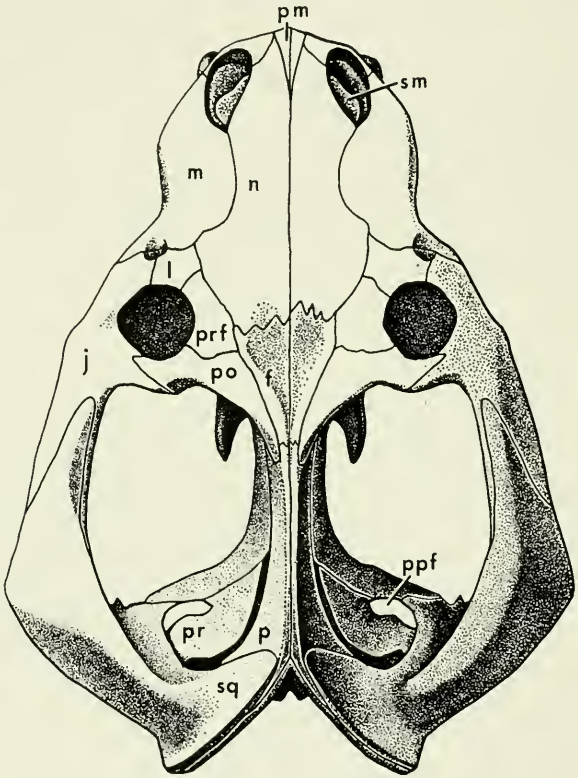

Fig. 2. Restored dorsal view of the *Belesodon* skull, × ⅓. Abbreviations for Figures 2 – 8: *bo*, basioccipital; *bs*, basisphenoid; *d*, dentary; *e*, epipterygoid; *f*, frontal; *fo*, fenestra ovalis; *j*, jugal; *jf*, jugular foramen; *l*, lacrimal; *m*, maxilla; *n*, nasal; *oc*, occipital complex; *p*, parietal; *pap*, paroccipital process; *pl*, palatine; *pm*, premaxilla; *po*, postorbital; *pp*, postparietal; *ppf*, pterygo-paroccipital foramen; *pr*, prootic; *prf*, prefrontal; *pt*, pterygoid; *ptf*, postemporal fenestra; *sm*, septomaxilla; *sq*, squamosal; *t*, tabular.

anteriorly, but the presence of a parietal foramen is doubtful. The condition of the specimen shows clearly that the parietals diverge posteriorly to take part in the occipital crests, clamped between the squamosals anteriorly and the postparietal posteriorly. On the occipital surface, sutures between the occipital complex and the adjacent dermal elements are difficult to determine.

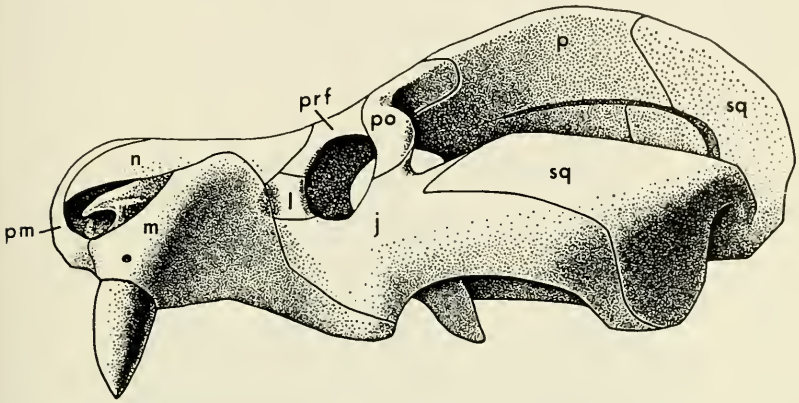

Fig. 3. Restored lateral view of the *Belesodon* skull. × ⅓.

Except for highly developed canines, the teeth are represented only by their sockets. There were the four incisors commonly present in cynodonts. The cheek teeth formed a somewhat curved row, turning outward posteriorly, where the maxilla extends somewhat outward and downward beyond the general line of the cheek. There appear to have been 12 cheek teeth, which presumably had the posteriorly curved tips seen in other chiniquodontids. The secondary palate is greatly elongated beyond the limits seen in non-chiniquodontid cynodonts. The posterior end of the secondary palate is somewhat incomplete on the left side; I have restored it to the condition seen on the right. The maxillary-palatine suture is obscured, but it is obvious that a great part of the secondary palate is formed by the palatines. For a short distance at the posterior end, the secondary palatal plate projects freely backward without being tied in at either side to the primary plate of the palatine. The posterior end of the vomer is presumably present in the roof of the choanal region, but its sutural separation from the pterygoid is obscure. The typical posteriorly-projecting "finger" of the palatine is present on either side of the primary palate,

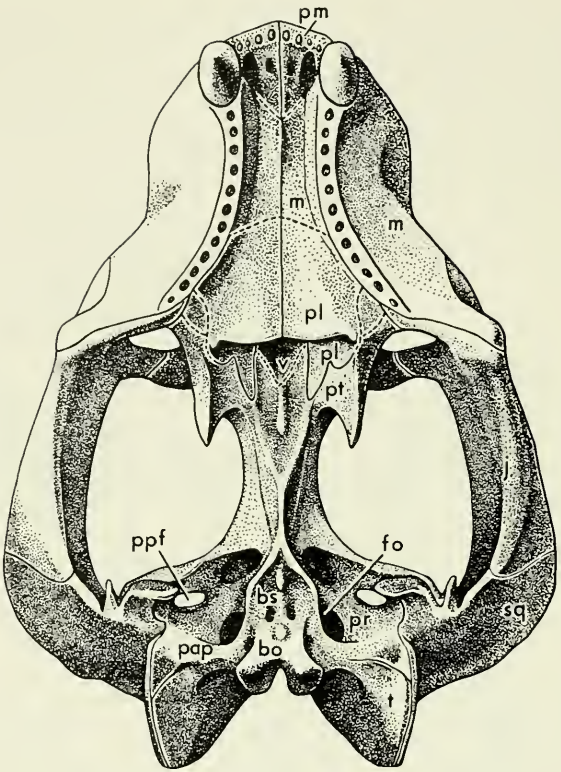

Fig. 4. Restored palatal view of the *Belesodon* skull. × ⅓.

separating medial and lateral palatal areas of the pterygoid. The boundaries of the ectopterygoid — presumably present but small — cannot be determined. On either side of the primary palate, a distinct longitudinal ridge is present at the line of suture between palatine and medial palatal ramus of the pterygoid. These ridges continue backward along the pterygoids, gradually converging posteriorly. A slight medial ridge is present at the line of suture between the two pterygoids. Ventrally-projecting flanges from the two pterygoids are highly developed.

The parasphenoid-basisphenoid region appears to have a normal cynodont structure, but the bone is somewhat imperfect. The ventral suture between the sphenoid and the occipital complex is

obscure. At about the position where this suture would be expected, somewhat anterior and medial to the jugular foramina, are a pair of pits which may be foramina. The ventral braincase surface is imperfect lateral and anterior to the fenestrae ovales. On the lateral surface of the braincase, relations of the prootic to adjacent elements are none too clear, but, as is usual in cynodonts, there is evidence of a groove for a vein lying between the prootic below and the squamosal and parietal above. The quadrates (as is all too common in cynodont specimens) are missing.

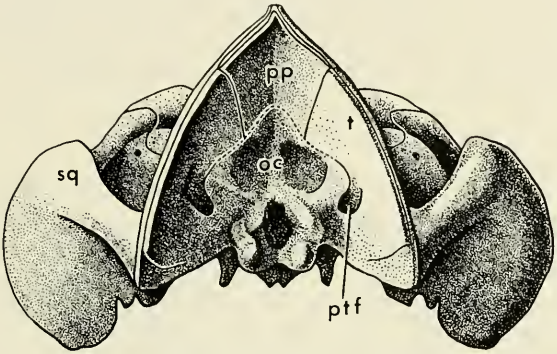

Fig. 5. Restored occipital view of the *Belesodon* skull. × ⅓.

CHINIQUODON
(Figs. 6-9)

As noted above, *Chiniquodon* was founded on a very incomplete skull, poorly preserved and poorly illustrated. The Harvard specimens add very considerably to our knowledge of this genus. They include two skulls (MCZ 3614 and 3615), a pair of mandibles, and some postcranial materials. Of the two skulls, MCZ 3614 measures 152 mm in length to the occipital condyles; MCZ 3615 is imperfect in the premaxillary region, but appears to be very closely comparable in size. The type skull would appear to have been about 140 to 145 mm, if complete. The two Harvard skulls are thus very close to the type in size and, further, appear to match the type closely in such features as Huene was able to describe. The skulls, like that of *Belesodon*, show a "crackle-ware" pattern which makes interpretation difficult. As in the case of *Belesodon*, I have attempted to present figures of the skull in which the "crackle-ware" effects are eliminated and in which breaks and

effects of crushing and distortion have been eliminated. The skull roof is rather well preserved in MCZ 3614, but little can be made of the palate. In contrast, the roof is not too good in MCZ 3615, but most of the palatal structure can be readily made out. MCZ 3615 has undergone strong lateral crushing. MCZ 3614, on the contrary, appears broad and relatively flat, so that dorsoventral crushing might be suspected. However, this is apparently not the case, for the braincase at the level of the parietal crest is as high in MCZ 3614 as in MCZ 3615.

My figures are based on a synthesis of features seen in the two skulls; the dorsal surface, arches, and occiput conform mainly to MCZ 3614; the palate and ventral portion of the braincase derive almost entirely from MCZ 3615. As in *Belesodon,* the general

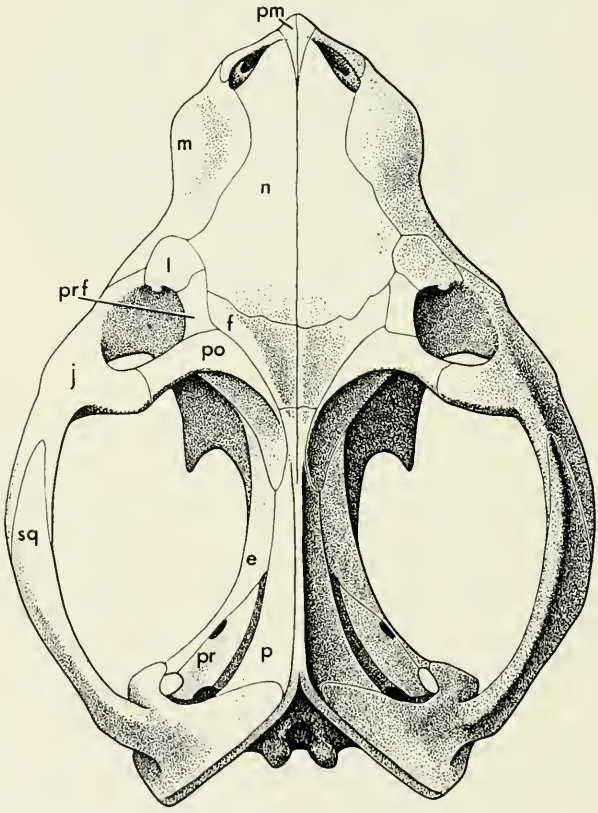

Fig. 6. Restored dorsal view of the *Chiniquodon* skull. × ⅔.

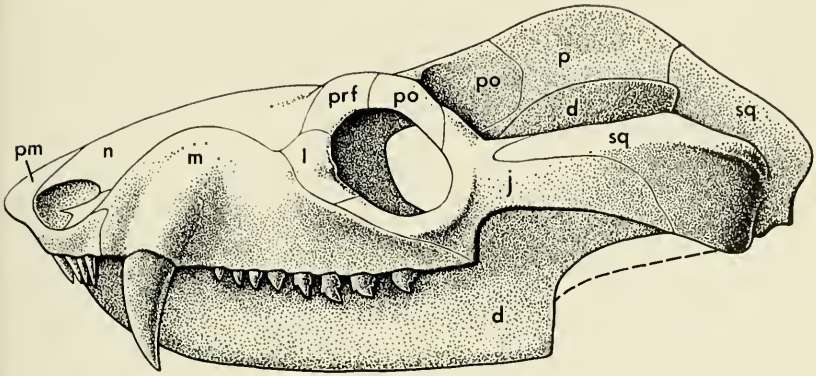

Fig. 7. Restored lateral view of the *Chiniquodon* skull. × ⅔.

proportions are comparable to those of thrinaxodonts. In neither skull are the ascending processes of the premaxillae, separating the nostrils, preserved; however, their slender distal tips are seen in MCZ 3614 between the nasals. The narial region is present only in MCZ 3614, but even here is damaged and the septomaxillae displaced and crushed, so that pattern in the region of the external nares is somewhat doubtful. As in *Belesodon*, the maxillae arch far dorsally around the roots of the canines; the canine swellings are not as marked as in *Belesodon* except posteriorly, where there is a sharp contraction in cheek width. The posterior end of the maxilla, beneath the orbit, projects very distinctly below the general contour of the cheek. The large nasals and the shorter, triangular frontals, ridged on either side by the postorbitals, compare closely with those of *Belesodon*. As in that genus, the crests of the two parietals are separated anteriorly for a short distance, but details are too imperfect to be sure whether or not a vestigial parietal foramen was present. The parietals continue backward conjoined in a high crest. Its summit is thinner than in *Belesodon*, and the two bones more closely appressed than in that genus, so that little trace of a median suture can be made out. The condition of the specimen is such that it cannot be determined how far the parietals extend posterolaterally into the occipital crests.

Of the circumorbital elements, the prefrontal occupies a modest area above the orbits; its boundaries are none too clear. The equally small lacrimal is situated below it on the anterior orbital border; a small but distinct protuberance extends back over the orbital rim external to the lacrimal foramen. Anterior to this point

there is a slight depression in the contour of the face, but this is much more shallow than the rather deep pit which appears to be present in *Belesodon*. The jugal is, as customary, a large element. Its slender anterior end lies between lacrimal and maxilla just anterior to the orbit; posteriorly it expands beneath the orbit to extend most of the length of the zygomatic arch, reinforced externally by the squamosal. It forms the lower part of the postorbital arch; its suture with the postorbital bone is indistinct. This last element forms most of this arch. On the dorsal surface it extends slightly farther forward than in *Belesodon*, and then with a dorsal ridge, swings backward to sheath the parietal laterally for some distance. The squamosal has the typical cynodont pattern of

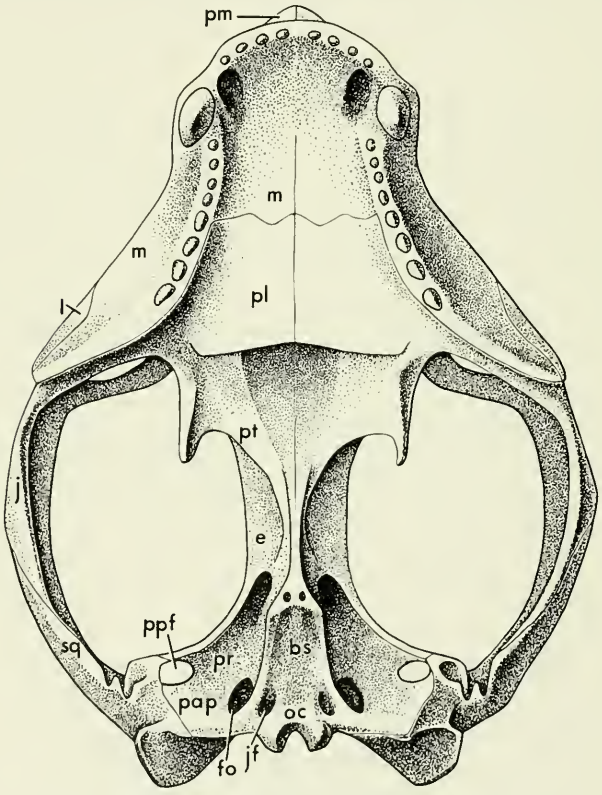

Fig. 8. Restored palatal view of the *Chiniquodon* skull, × ⅔.

two semi-distinct parts. The zygomatic arch ramus constricts posteriorly to join the more medial segment of the bone with a relatively narrow neck far down the side of the skull. The medial ramus extends from the back end of the sagittal crest as a broad sheet of bone which, sheathing postparietal and then tabular anterolaterally, curves outward and downward along the anterior surface of the occipital crest. The details in the region of the quadrate (which is absent) and of the paroccipital process are not well preserved; clearly seen, however, is the thickened area of the squamosal which runs downward along the ventromedial margin of the occipital ramus, lateral to the prootic, to strengthen the inner end of the quadrate region.

In MCZ 3615 the occiput is strongly compressed laterally; the proportions are more normal in MCZ 3614, although there is a slight spread ventrally between the occipital crests. In neither specimen are details well preserved, and sutures are obscured.

Almost nothing can be made of the palate of MCZ 3614, and reliance must be placed on MCZ 3615. Even here, the anterior part of the palate is in none too good condition; however, except for the palatal exposure of the premaxillae, the general structure is clear, although the breadth may have been somewhat less than I have figured it. The secondary palate here is developed to the same major extent as in *Belesodon,* with the palatines playing a major part in it. Details of the primary palate posterior to the end of the secondary palate are obscure as to sutural relations of pterygoids, ectopterygoids, palatines, and vomers. There are well-developed pterygoid flanges, but these are less prominent than in *Belesodon.* Posterior to the contraction of the palatal structures into the basicranial "girder," the ventral braincase structures, of proper cynodont character, are clearly discernible. The lateral walls of the braincase are somewhat imperfect in both specimens, but are rather better preserved in MCZ 3614 . The parietal above, the squamosal posteriorly, and the pterygoid ventrally, with the epipterygoid and prootic filling out the side walls of the braincase area, appear, as far as can be determined, to form a typical cynodont pattern. The distal end of the quadrate ramus of the epipterygoid is unfortunately imperfect.

Of the premaxillary-maxillary dentition, MCZ 3614 shows the four customary incisors, here of small size, broadly spaced across the arch formed by the premaxillae. The canines are stout; one, measuring 20 mm in its exposed portion, is completely preserved. The cheek teeth are moderately well preserved in MCZ 3615. The two series begin anteriorly somewhat medial to the canines and

extend backward, diverging at an angle of about 35°-40° to each other, well below the level of the secondary palate; the rows are nearly straight for most of their extent, but curve somewhat outward posteriorly. On the right side of MCZ 3615 a small anterior alveolus is followed by eight teeth; on the left, there are eight teeth, with posteriorly an alveolus in which a ninth tooth was forming. As in carnivorous cynodonts in general, the teeth are oval in shape at their bases; subcircular in the case of the small anterior teeth, elongate anteroposteriorly in the more posterior members of the series. The crowns are almost all lacking in MCZ 3614, are rather imperfect on the left side of MCZ 3615, but in fairly good shape on the right side of the latter specimen. The first three appear to have single cusps. The fourth and fifth teeth are imperfect, but the fourth appears to have an accessory posterior cusp, and the fifth definitely has a small anterior accessory cusp as well. On tooth six, the anterior cusp is somewhat medial but remains small; the posterior one is becoming larger. In teeth seven to nine the posterior cusp is very prominent, and has divided to give off a secondary posterior cusp near its base. The anterior cusp persists in teeth seven and eight, and extends posteriorly on the medial surface in cingulum fashion on the former. It has disappeared in the last tooth. The tips of the main cusps of teeth five through seven are incomplete, but in teeth eight and nine, this cusp is complete and is seen to be curved sharply backward.

With the skulls was found a conjoined pair of lower jaws, poorly preserved, much "crackled," and incomplete posteriorly. The jaws are of a size appropriate to the skulls. The large dentary is nearly completely preserved, except for its posterior tip. The splenial is present, but there are few identifiable remains of other postdentary elements. The angle of the dentary is sharply marked and thickened ventrally. The symphysis is, as expected, extremely stout. On the inner surface of the ramus, traces of the meckelian groove between dentary and splenial are visible anteriorly. Posteriorly, the outline of the hollow (sharply defined dorsally), which should house the surangular, is visible. The dentition is poorly preserved. There appear to have been three incisors in front of the stout canines. The lower postcanine tooth row forms a nearly straight line on either side, the two rami diverging at an angle of about 40°. The area for the roots of the cheek teeth forms a very distinct swelling along the upper part of the inner surface of the dentary; this swelling — and the tooth row itself — extends to a point a short distance back of the base of the ascending ramus.

Little can be made of the cheek tooth series except that all were thin-oval in section and compressed lateromedially, and that the more posterior ones were, as expected, longer anteroposteriorly than the smaller anterior ones. There are eight members in the series.

A collection of postcranial elements of appropriate size (Fig. 9) was also found with the two skulls. A number of disarticulated vertebral centra had diameters of 12 to 16 mm, and lengths of 10 to 14 mm. Two scapulae were present, with heights as preserved of 72 and 81 mm; with one were associated a pair of coracoidal elements. The shoulder girdle is of a typical cynodont pattern. Two complete and a third, incomplete, humeri are present. A left humerus, with a length of 78 mm, is essentially perfectly preserved. It is of a typical cynodont type, but is relatively short and stout as compared with that of *Diademodon*, for example; in that form, the distal width is but slightly over half the length, whereas here this figure is just short of 60 per cent. Associated in the beds with this material was a tiny humerus, obviously that of a "youngster." As preserved, it measures 29 mm in length. The distal end is not preserved and was presumably poorly ossified, if ossified at all; even if allowance be made for this situation, the total length in life would have been but approximately 40 per cent that of the more adult specimen described.

A disarticulated right ilium is nearly complete, except for the posterior tip of the blade, but is badly battered and cracked. Its breadth across the articular areas for pubis and ischium is 34 mm. The supra-acetabular buttress is highly developed, extending outward some 11 mm over the deepest part of the acetabulum. A small but very distinct pocket is present on the outer surface of the ilium, close to the acetabular margin, just in front of the buttress. The greatest length of the iliac blade, as preserved, is 55 mm. Two ischia are present; the better preserved is illustrated, reversed, in articulation with the ilium. There is a very distinct posteriorly-facing surface for the iliotrochantericus.

A left femur, with a length of about 80 mm, is, in general, of typical cynodont type, slender in build (as compared with the stout humerus), with a proximal width across the head and greater trochanter of 32 mm, a shaft diameter of 9 mm, and a distal width of 23 mm. As typical of the cynodonts, the dorsal surface of the head is flattened and, indeed, somewhat concave in section. There is a distinct, if shallow, intertrochanteric fossa, and a distinct internal trochanter from which a pronounced adductor ridge extends nearly half the length of the bone. Distally, there is little

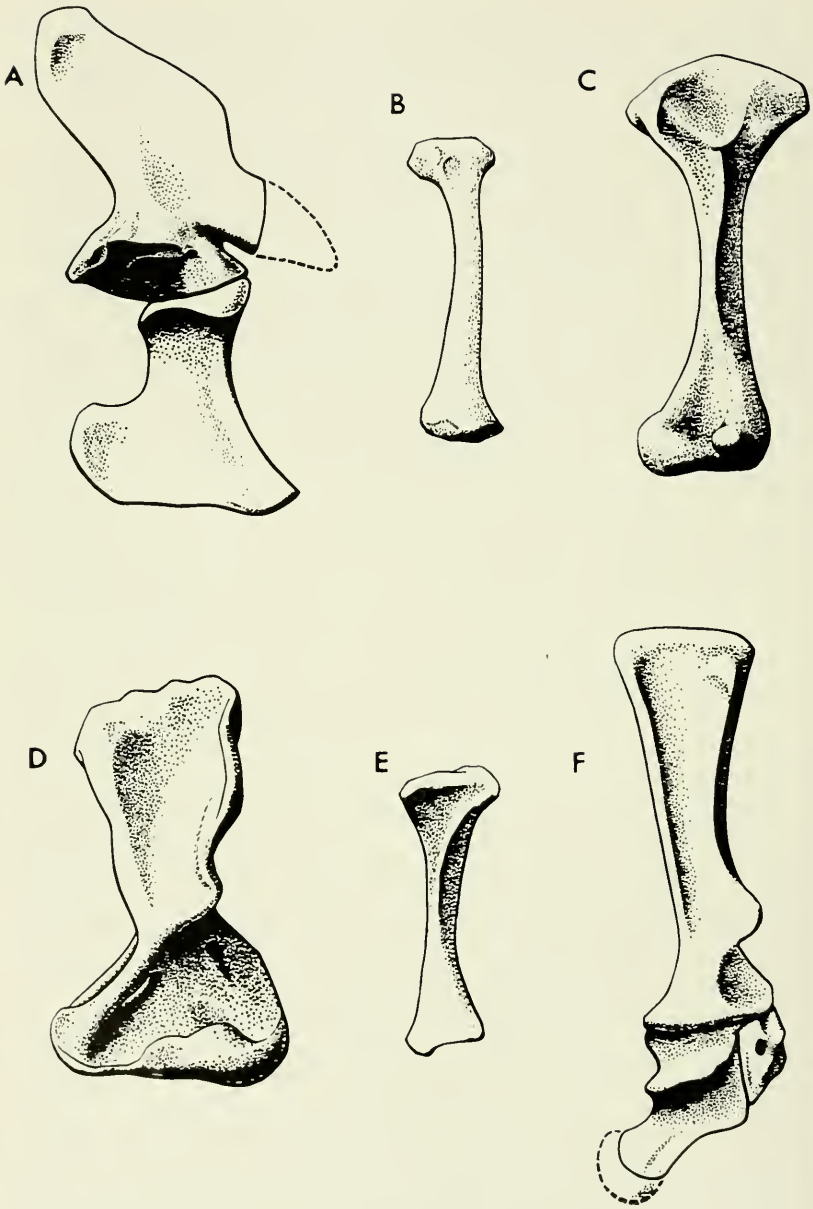

Fig. 9. Postcranial elements found with the *Chiniquodon* skulls. × ⅔. *A*, left ilium and ischium; *B*, fibula; *C*, femur, ventral aspect; *D*, humerus, ventral aspect; *E*, tibia, flexor aspect; *F*, scapulocoracoid.

development of an intercondylar fossa on the dorsal surface. Ventrally, the two articular areas for the tibia are very highly developed and rounded; the articular areas face essentially distally, indicating a more extended average position of the tibia than in more primitive forms. Two tibiae and one fibula are present. The tibiae have slender shafts but expanded termini. The right tibia, the better preserved of the two, measures 57 mm in length, with widths proximally of 14 mm, midway of the shaft 7 mm, distally 17 mm. The cnemial crest is sharply developed. A thin ridge, most prominently developed proximally, is present along the lateral edge of the shaft for about a third of its length, beginning a short distance below the head of the bone. The fibula preserved is 59 mm long. The head is broadened but flattened in primitive fashion; the distal articular surface, stout and convex in shape, is 15 mm wide.

In the Museum of Comparative Zoology collections is a small cynodont skull, MCZ 3035, collected by Price in the Candelária region, measuring 65 mm in length. Little detail can be made out, but there is evidence of cheek teeth of a recurved, chiniquodontid type, and the specimen seems surely a juvenile of either *Chiniquodon* or *Belesodon*.

DISCUSSION

Despite imperfections in the materials, the skulls figured and discussed above give us a much better picture of the cranial anatomy of *Belesodon* and *Chiniquodon* than could be obtained from Huene's specimens. It is obvious that these two forms are closely related, as Huene believed to be the case, and have a number of distinctive characters in common, notably the remarkable development of the secondary palate. Watson and I (1956) and Lehman (1961) suggested their inclusion in the Cynodontidae. But they do not show any indication of derivation from typical members of that family. Their general proportions and some details (such as dentition) indicate alliance with, and derivation from, the Thrinaxodontidae, as suggested by Bonaparte (1966), but the notable advance in the palate seems in itself justification for Huene's having erected for them the family Chiniquodontidae.

Are *Belesodon* and *Chiniquodon* so closely related that they should be placed in the same genus? The answer is not clear. No great weight should be given to minor differences between the two skull types as figured here, since, as I have pointed out, the skulls on which my illustrations are based are imperfect, and seeming differences may be due in part to misinterpretations of the data or differential crushing. On the whole, I believe it better to maintain their distinction until further and better materials are available.

It might further be suggested that *Chiniquodon* and *Belesodon* are merely growth stages of the same form, and that differences such as the greater number of cheek teeth in *Belesodon* are merely a function of age and increase in size. This is possible but, I think, unlikely. It is probably no coincidence that, in the case of Huene's materials from Chiniquá and ours from Candelária, the specimens found are distinctly members of two size groups. Although it is known that in cynodonts the length of the dental battery may increase with additions to the tooth number, the maxillary structure of *Chiniquodon* is such that it is difficult to see how several further teeth could be added posteriorly. Apart from lack of fusion of elements of the shoulder and pelvic girdles, there is little evidence of immaturity in the known *Chiniquodon* material. For example, the humeri of this form, described above, are essentially completely ossified, with apparently little cartilage at either end. They seem sufficient (but barely sufficient) to function in an animal of the proportions indicated by the *Chiniquodon* skulls; but it is impossible for such a humerus to have grown to the size necessary for support of an animal of the bulk indicated by the *Belesodon* skulls.

In sum, I think it best in the present state of our knowledge to consider *Chiniquodon* and *Belesodon* as distinct but closely related, and to provisionally retain the two as members of sympatric genera.

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CAMBRIDGE, MASS. 24 OCTOBER, 1969 NUMBER 333

THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA V. A NEW CHINIQUODONTID CYNODONT, *PROBELESODON LEWISI* — CYNODONT ANCESTRY

Alfred Sherwood Romer

ABSTRACT. A carnivorous cynodont from the Middle Triassic Chañares fauna of Argentina is described as *Probelesodon lewisi,* gen. et sp. nov. This is an advanced cynodont with an elongate mammal like secondary palate, related to the chiniquodontids of the Santa Maria Formation of Brazil. The short face and recurved molars indicate descent from thrinaxodontids rather than the Cynognathidae. Cynodont ancestry is discussed. There is no evidence of derivation from scaloposauroids and presumably the cynodonts are of independent descent from the ancestral theriodonts.

INTRODUCTION

As is generally recognized, a marked change took place during the Triassic in the nature of the terrestrial predaceous vertebrate fauna. In the early Triassic Karroo beds carnivorous therapsids are dominant; in the late Triassic, therapsids (except those which have progressed to the mammalian stage) are practically extinct, and archosaurs — thecodonts, crocodilians, dinosaurs — have replaced them as the major carnivores. Until recently, Middle Triassic terrestrial vertebrate faunas were almost unknown, but it would be expected that, at that time, there would have been transitional conditions, in which predaceous therapsids would be undergoing reduction, and archosaurs, on the other hand, would be increasing in abundance and diversification.

Our currently increasing knowledge of the excellent series of Middle Triassic beds of South America shows that this is indeed the case. The faunas of this age now known from that continent form a sequence including, in descending order, assemblages present in these three formations: Ischigualasto (Argentina), Santa

Maria (Brazil), and Chañares (Argentina). In these beds, predaceous cynodonts are undergoing sharp reduction. In the uppermost of the three faunas, that of Ischigualasto, only a single fragmentary specimen of a carnivorous cynodont has so far been recovered (Bonaparte, 1966). In the extensive collections made by Huene (1944) in the Santa Maria beds, there were but two carnivorous cynodonts, each represented by a single specimen; further collections made for Harvard and the American Museum included only a very few additional individuals. But when we descend to the lowest of the three faunas, that of the Chañares Formation, we find that cynodont reduction is relatively less marked. Only two predaceous members of that group are present, but they are moderately abundant. Our collections include more than a score of specimens.

The present work is limited to a description of the cranial anatomy of the larger of the two forms present. I plan shortly to publish on the cranium of the second cynodont, and later, on postcranial materials of both forms.

The cynodont here described may be formally named and characterized as follows:

PROBELESODON LEWISI gen. et sp. nov.

Combined generic and specific diagnosis. A chiniquodontid cynodont, closely related to *Belesodon* and *Chiniquodon,* but of smaller size than the former, the more mature individuals reaching an average skull length, from snout to condyles, of about 140 mm; the secondary palate long; generally with nine maxillary cheek teeth, the "molars" multicuspidate, the main cusp backwardly curved.

Holotype of the species. No. 64-XI-14-6, La Plata Museum, a skull and jaws collected from the Chañares Formation in La Rioja Province, Argentina, about 10 km east of the point where the Río Chañares emerges into the Plano de Talampaya.

The generic name is due to the obviously close relationship, discussed later, of this form, to *Belesodon* (and *Chiniquodon*) of the somewhat later Santa Maria beds; the specific name is given in honor of Arnold D. Lewis, chief preparator at the Museum of Comparative Zoology, who played a major part in the collection of the Chañares material.

I am indebted to National Science Foundation Grant GB-2454 for aid in collection of the material and Grant GB-8171 for its preparation and for publication costs.

THE SKULL

(Figs. 1-5)

Of *Probelesodon,* nine skulls have so far been discovered. Of these, five representing apparently mature individuals are members of a single size group, with lengths from premaxillae to condyles in four of them measuring: 143, 137, 132, and 130 mm (a fifth member of this group is incomplete posteriorly). A skull which is incomplete in the occipital region is obviously larger and probably measured about 155 mm in length. The holotype, on the other hand, is somewhat smaller, with a basicranial length of 115 mm. It is probably somewhat immature; it may be noted that a replacement of canines is taking place. Two "juveniles" have been found. One measures 72 mm in length; the second lacks the occiput but was of approximately the same size.

In general proportions, the skull resembles certain of the thrinaxodontids and differs from such well known forms as *Cynognathus* and *Diademodon* in its relatively short muzzle and broadly flaring zygomatic arches, the width across the arches reaching 75 to 80 per cent or more of skull length. Anterior to the external nares the skull terminates in a pointed snout. In cross section the muzzle is rounded, curving inward ventrally somewhat toward the tooth rows of the cheeks, although this ventral curvature is not so great as in, for example, the contemporary gomphodonts. In advanced fashion the sagittal crest is high and thin, as are the occipital crests. The zygomatic arches are moderately deep, but the arch and occipital crest connect only by a narrow waist, in contrast to the broad sweep of the squamosal connecting the two in many other cynodonts. The postorbital arch is narrow. The orbits are situated close to the half length of the skull. The parietal foramen appears to be generally absent; if perhaps present in some specimens, it is at best vestigial. As in other advanced cynodonts, the occipital condyle is definitely double. Most notable of distinctive characters is the great development of the secondary palate, unmatched in any other known cynodonts except the related chiniquodontids of Santa Maria.

In external exposure the premaxillae form the area of origin of the four incisors on either side, and the ventral and medial borders of the external nares. Conjoined processes of the two premaxillae extend upward and forward anterior to the nares to form the pointed snout tip and then, diminishing gradually in size, turn backward above as slender rods separating the nasals for a considerable distance. A septomaxilla is present, presumably of the

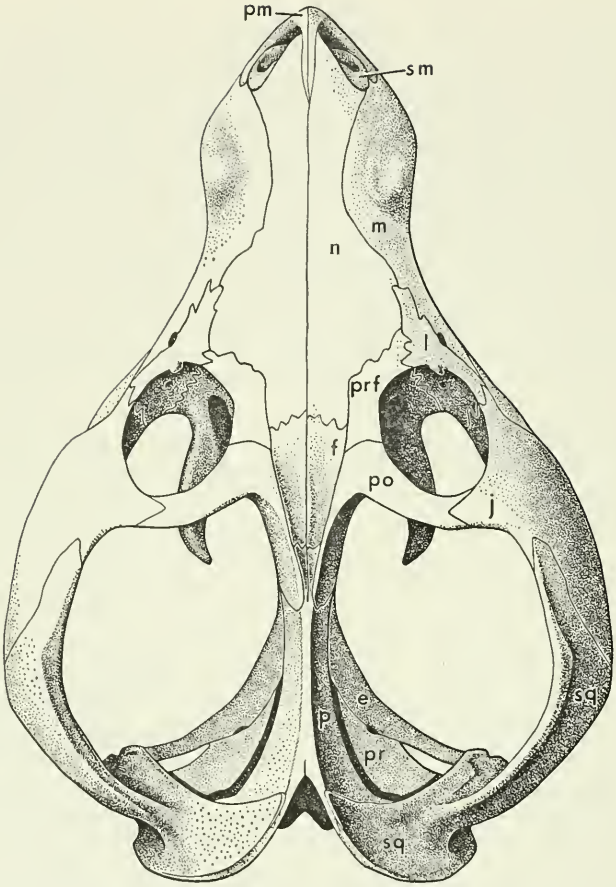

Fig. 1. *Probelesodon lewisi*, dorsal view of skull. This and the following figures of the skull and jaws are based primarily on the type, with supplementary data from other specimens. Figures 1-7 are the size of the type and approximately ¾ times the size of the largest mature specimens. Abbreviations for Figures 1-7: *a*, articular; *an*, angular; *bo*, basioccipital; *bs*, basisphenoid + parasphenoid; *d*, dentary; *e*, epipterygoid; *ec*, ectopterygoid; *f*, frontal; *fo*, fenestra ovalis; *j*, jugal; *jf*, jugular foramen; *l*, lacrimal; *m*, maxilla *n*, nasal; *oc*, occipital complex; *p*, parietal; *pap*, paroccipital process; *pl*, palatine; *pm*, premaxilla; *po*, postorbital; *pp*, postparietal; *ppf*, pterygoparoccipital foramen; *pr*, prootic; *pra*, prearticular; *prf*, prefrontal; *pt*, pterygoid; *ptf*, posttemporal fenestra; *q*, quadrate + quadratojugal; *sa*, surangular; *sm*, septomaxilla; *sp*, splenial; *sq*, squamosal; *t*, tabular; *v*, vomer; v_2 + $_3$, foramen for trigeminal nerve; *vg*, groove for a vein.

typical cynodont type, but was apparently loosely articulated, is frequently absent in the specimens and is never well preserved. The maxilla is a large element, extending from the narial region back along the side of the snout and, curving outward, has a somewhat thickened terminus, below the orbit, which projects notably below the level of the jugal arch. This contrasts with the pattern seen in such cynodonts as *Cynognathus* and *Diademodon*, in which a suborbital projection is formed by the jugal rather than the maxilla. Behind the naris, the maxilla, in relation to the obviously deep root of the canine, extends, in contact with the nasal, far up the snout toward the midline; posterior to the canine region, its margin turns downward again, bordered posteriorly by the lacrimal and jugal, to terminate at the ventral process mentioned above. Several small foramina penetrate the maxilla, and an especially large one is present between the maxilla and the lower border of the lacrimal. The region containing the canine root is prominently swollen, and the face is expanded ventrally at the region of the emergence of the canine. The canine swelling is especially prominent in the larger specimens, and there tends to develop a clearly marked channel curving around the base of the canine root.

Of the median roofing elements, the nasals, as in cynodonts generally, are very long; here they reach back half the length of the skull roof to terminate between the orbits. They form the upper margins of the nares; continuing backward between the maxillae, they are somewhat constricted in width in the region of the canine roots. They expand laterally to bound the dorsal margins of the lacrimals, and then constrict again between the prefrontals to a nearly directly transverse suture with the frontals. Since this suture is considerably farther posterior than is common in therapsids, the frontals are reduced in length and area, and are essentially a pair of triangular wedges, separated suturally from the postorbitals between and below backwardly converging ridges. The frontals appear to be exposed laterally within the orbital rim, between prefrontals and postorbitals. The parietals have as a main function the formation of a high median sagittal crest. For most of their length, the two are solidly fused at the narrow tip of the crest. Anteriorly, they diverge slightly for a short distance. The parietals descend some distance down the gradually diverging sides of the sagittal crest, overlapped anteriorly by the postorbitals. Posterior to the postorbitals the lower margins of the parietals extend backward along the line of the vein whose course can be often followed in cynodonts, bounded below by the epipterygoid

and the prootic region of the braincase. In contrast to conditions in some other cynodonts, the venous channel and the parietal-epipterygoid boundary seem to coincide. There is visible here, in some specimens, an unossified area, presumably cartilage-filled in life, between parietal above and prootic below. As in cynodonts generally, the two parietals diverge posteriorly to take part in the formation of the occipital crests.

Of the series of circumorbital elements, the lacrimal occupies much of the anterior margin of the orbital rim and extends forward and upward as in cynodonts generally, to gain a contact with the nasal as well as having the normal external contacts with the prefrontal dorsally, maxilla anteroventrally, and jugal posteriorly at the lower orbital margin. The bone also forms a portion of the ossified anterior surface of the orbital socket, between prefrontal above and jugal below. Ventrally in the orbit, the lacrimal has a firm connection with the dorsal surface of the palatine. On the orbital rim, external to the lacrimal foramen, there tends to develop an osseous protuberance, most prominent in the large specimens, the function of which is uncertain. The jugal is, as usual, highly developed. Dorsally, it forms part of the relatively narrow postorbital bar; anteriorly, it extends forward below the orbit to meet the maxilla and lacrimal and internally forms the most ventral part of the orbital wall. Anterointernally, it gains a contact with the ectopterygoid and pterygoid at the lateral margin of the palatal plate. As noted above, there is no development of a suborbital process of the sort seen in *Cynognathus, Diademodon,* etc. The main ramus of the jugal extends posteriorly to form a great part of the substance of the deep zygomatic arch. It reaches posteriorly and ventrally nearly to the posterior root of the arch, although sheathed externally over most of its course by the squamosal. The postorbital forms the upper part of the postorbital bar, and extends somewhat anteriorly and medially on the skull roof. Posteriorly on the roof, a pair of flanges from the postorbitals, ridged on their medial margins, extend backward from the prefrontals, constricting the frontals between them. Below these dorsal processes, the postorbitals extend backward on either side of the base of the sagittal crest for some distance, sheathing the parietals externally. The prefrontal has a modest external exposure along the upper orbital margin, bounded medially by the nasal and frontal, anterolaterally by the lacrimal, posteriorly by the postorbital. Internally, it continues upward the orbital wall formed more ventrally by lacrimal and jugal and dorsomedially by the frontal.

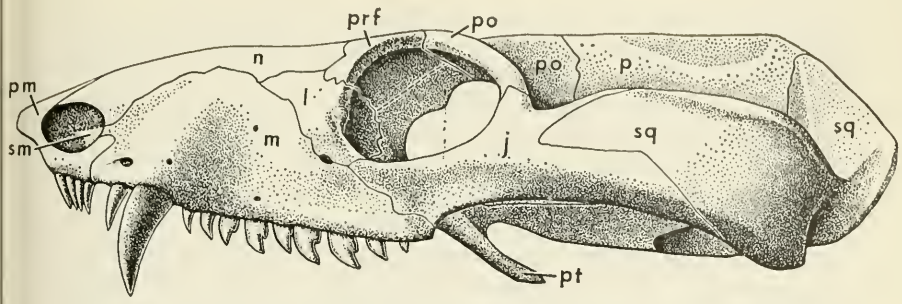

Fig. 2. Lateral view of the skull of *Probelesodon lewisi.*

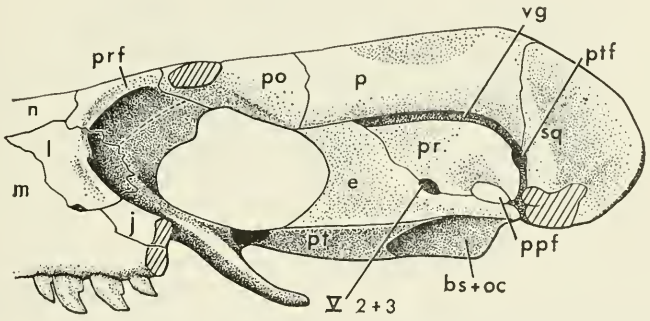

Fig. 3. Lateral view of the skull of *Probelesodon lewisi,* with the zygomatic arch removed.

The squamosal is one of the largest as well as the most complex of cranial elements. It consists of two major rami, the two connected by a relatively narrow neck, contrasting with the broader connection seen in many cynodonts. The external ramus plays a prominent part in the formation of the zygomatic arch, covering much of its outer surface and, at the posterior end, forming its entire thickness. Anteriorly, it ends in a slender external tongue not far behind the base of the postorbital bar. A short distance back of this point, it reaches the upper margin and retains this position for the length of the arch; broken specimens show that

the upper portion of this squamosal ramus is received in a deep longitudinal groove in the underlying jugal. The upper margin is distinctly thickened. Posteriorly, as the arch curves downward and inward, the upper external surface of this ramus is somewhat channeled longitudinally, with a mildly concave cross-section. This channel corresponds to the much more marked channel in *Cynognathus* which has been interpreted as an external auditory meatus. At the posterior portion of the arch, the lower margin of the squamosal extends downward over the entire width of the jugal and, extending still further downward, forms a somewhat thickened flange covering the posterior portion of the mandible. There is no indication of any specialized surface for articular contact with the dentary, which lies just internal to this flange.

The occipital ramus of the squamosal forms mainly a thin sheet of bone which occupies the anterolateral surface of the occipital crest. At the upper end of the crest, it covers the posterior end of the parietal, and more distally is obviously applied to the anterior faces of the postparietal and tabular. On the anterior face of the occipital crest, the squamosal is separated from the prootic surface of the otic capsule by an unossified gap, presumably cartilage-filled in life, along the line traversed by the vein mentioned earlier as separating parietal and epipterygoid. Toward the outer (and lower) part of the occipital crest, this unossified line of separation increases in breadth. Present here is the anterior opening of the posttemporal fenestra.

In the region of the junction of its two rami, the squamosal has a complex structure. At the forward curving lower termination of the occipital ramus, its lateral margin turns ventromedially, and buttresses the end of the paroccipital process. This area is somewhat concave in external surface; it is the lower end of the presumed auditory meatus, and hence the margin of the squamosal here, together with the adjacent quadrate and articular, may have afforded support for a tympanum. Anteriorly and laterally to this area, the squamosal is specialized for support of the quadrate. The lower margin of the zygomatic arch at its medial end, adjacent to the flange mentioned earlier, shows the typical pair of notches in which the quadrate (with the quadratojugal) was loosely inserted. On the anterior face of the occipital ramus, a thickened area develops at its outer end; this thickened portion descends anterolaterally to aid in forming a socket, facing ventrally, in which lay the main body of the quadrate.

In posterior view, the occiput is essentially triangular in shape, with the apex dorsally at the point where the sagittal crest bifurcates in formation of the occipital crests, and with a nearly flat base formed by the lower part of the occipital complex, with the stout paroccipital processes extending out nearly directly laterally. The two tall occipital crests diverge at nearly a right angle to extend backward and outward and, curving downward, terminate in the area of the jaw articulation. The point of divergence is situated much farther forward than in most earlier cynodonts. As noted above, the parietals extend some distance down the occipital crests. The anterior surface of the crests is formed by the squamosals; the posterior surface is composed of the postparietal medially and the paired tabulars laterally. The tabulars extend

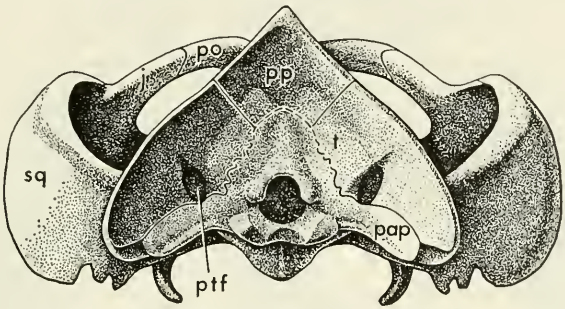

Fig. 4. Occipital view of the skull of *Probelesodon lewisi*.

downward to cover much of the paroccipital processes; the lower parts of these processes, however, are exposed posteriorly. The posterior openings of the posttemporal fenestrae lie above the paroccipitals, within excavations in the ventromedial border of the tabulars. Sutures between the three dermal elements and the occipital complex, which occupies the central area of the occiput, are generally obscure. The occipital elements are fused, without visible sutures; ventrally the occipitals carry the distinctly paired condyles and surround the foramen magnum. On either side of this foramen there are slight swellings which suggest a proatlas articulation.

The anterior end of the palatal surface is formed by the premaxillae. These bones afford insertion for the "incisor" teeth. These lie in the form of a widely opened arch. Close to the midline are the long but very narrow incisive foramina, whose boundaries appear to be entirely formed by the premaxillae; I see no

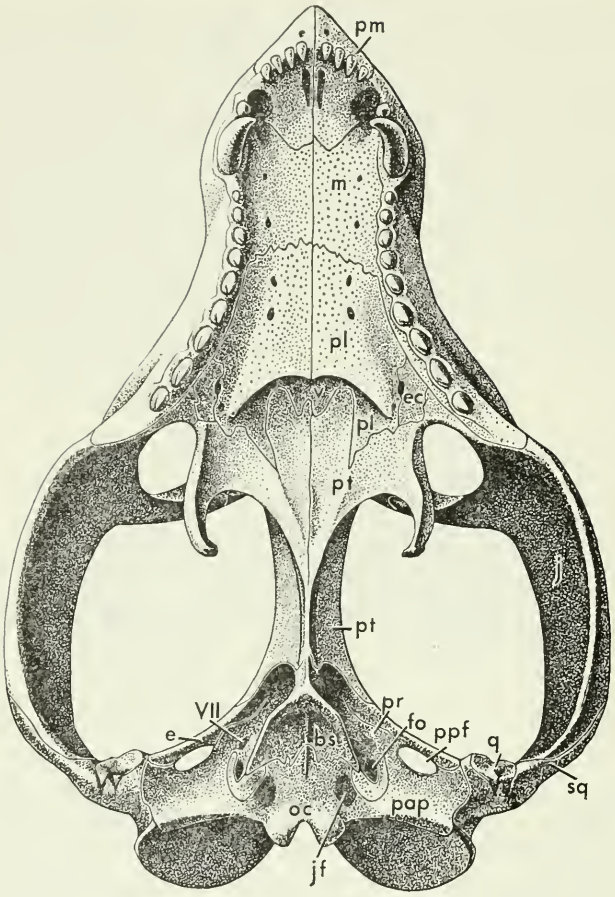

Fig. 5. Palatal view of the skull of *Probelesodon lewisi.*

evidence of the presence of the vomer here. From a point back of the posterior end of the incisive foramina, the sutures between premaxillae and maxillae run laterally, to become lost in the very deep pockets for the reception of the large lower canines. Back of this area stretches the long secondary palate. Approximately half of this structure is formed by the maxillae. On either side of the palate the maxillae form a broad base for the insertion of the cheek tooth series. Anteriorly, the inner margins of the two rows approach one another somewhat more closely than might be

allowed by muzzle width; posteriorly, the tooth rows curve outward in typical cynodont fashion, so that at the back end of the dental series the palatal width is about twice that of its anterior portion. Anteriorly, the tooth bases are close to palatal level; posteriorly, on either side, the inner margin of the maxilla forms a distinct shelf, bearing the line of tooth bases well below the level of the palate. The secondary palate is continued backward to a remarkable degree by the palatines. The palatine portion of the secondary palate is somewhat arched and convex ventrally in transverse section. Posteriorly, the secondary palatal structure does not expand laterally; hence the most lateral portions of the palate here (mainly the ectopterygoid areas) are not involved, and lie at a somewhat higher level than do the palatines. The thin posterior margin of the secondary palate is often broken, but appears to have been somewhat concave in outline as seen from below. Both maxillary and palatine portions of the secondary palate show several pairs of small foramina; a particularly large pair is present at the palatine-ectopterygoid suture.

The secondary palate development here is in strong contrast to that of all other described therapsids (except other, related, chiniquodonts), in which only the most anterior parts of the palatines are involved. In the extent of the secondary palate, the chiniquodonts rival mammals.

Beneath the posterior end of the secondary palate can be seen the posterior end of the vomer. On either side is visible a portion of the palatine forming part of the primary palate; posteriorly, there extends a long finger of the palatine overriding the pterygoid. Lateral to the posterior end of the secondary palate, a small ectopterygoid is persistent, bounded by palatine, maxilla, jugal, and pterygoid. Medial to the distal end of the maxilla, an extension of the jugal runs inward and forward to a contact with ectopterygoid and pterygoid.

There persists a considerable palatal ramus of the pterygoid. Each pterygoid extends forward medial to the palatine "finger" mentioned above, to gain contact with the vomer. Lateral to the palatine there is a second forward extension which gains contact with the ectopterygoid and, briefly, with the jugal. This region includes the area of the primitive pterygoid flange. In many therapsids, notably cynodonts, a ventral process tends to develop which apparently acts as a guide for the lower jaws. In specimens of the present species in which these processes are well preserved, they are more elongate than in any other non-chiniquodont described form.

From the palatine "fingers," ridges run back on either side to converge medially. Lateral to these ridges, the margins of the ventral surfaces of the palatal rami of the pterygoids likewise run back to form ridges parallel to those just described and gradually converging with them. More laterally, the pterygoids are exposed in the floor of the orbits and continue backward as a strip of bone joined dorsally with the epipterygoids. Posteriorly, the pterygoids fuse in the midline and clamp on either side the anterior end of the parasphenoid-basisphenoid complex, forming the median ventral "girder" characteristic of advanced cynodonts, which contrasts with the looser basal connection of palate and braincase present in more primitive synapsids. On either side of the ventral keel of this "girder" is a groove, presumably carrying a blood vessel, bounded externally by a longitudinal ridge. In this ventral region, sutures between pterygoids, epipterygoids, and basicranial structures are not clearly seen. It appears, however, that posteriorly each pterygoid bifurcates, a medial portion sheathing the lateral surface of the parasphenoid-basisphenoid for a short distance and the lateral branch swinging outward to accompany the epipterygoid toward the region of the jaw articulation. A thin plate of bone connecting the two portions forms the floor of the cavity equivalent to the anterior part of the primitive cranioquadrate passage. This passage presumably carried the carotid artery, lateral head vein (if present), and one ramus of nerve VII.

There has been no general agreement as to the relative extent of epipterygoid and pterygoid in the ramus extending toward and to the quadrate region. It is generally believed that the pterygoid is the dominant element here, and that the posterior extent of the epipterygoid is much restricted. The sutural situation in the *Probelesodon* material is obscure, but it seems more reasonable to conclude that here the quadrate ramus is primarily formed by the epipterygoid, and that the backward reach of the pterygoid is limited.

Behind the anterior orbital rim formed by lacrimal and prefrontal, there is a major gap in the side wall of the braincase — a gap filled, of course, in mammals by the orbitosphenoid and extensions of the adjacent dermal elements. Presumably the optic nerve, the eye muscle nerves, and nerve V_1, emerged through this gap. Behind the gap is, as in cynodonts generally, a greatly expanded epipterygoid, lying between parietal and postorbital dorsally and pterygoid ventrally. Its anterior boundary is concave as seen in side view. Posteriorly, it is in contact with the anterior border of the prootic portion of the ear capsule. This region is

not too well preserved in the material available, but there does not seem to be any appreciable epipterygoid overlapping of the prootic, although the suture between the two is an irregular one. Part way down the line of suture is a foramen which is believed to have transmitted nerves V_{2+3} (plus associated blood vessels). Ventrally, an extension of the epipterygoid runs backward and swings outward to the region of the quadrate and squamosal. The epipterygoid forms the anteroventral wall of the pterygo-paroccipital foramen, presumably for venous passage.

Although accommodations for housing the quadrate (+ quadratojugal) in the squamosal are present, as described above, this bone, loosely articulated, tends to drop out when the jaw is disarticulated. It is present in the material only in two cases in which the lower jaws are in place, and in consequence, its structure cannot be completely made out.

Although, as noted, sutural lines are none too clear in the region of the median longitudinal bar formed mainly by the pterygoids, it is obvious that the parasphenoidal rostrum, clamped more anteriorly between the pterygoids, becomes visible ventrally in the posterior part of this bar. The anterior end of the parasphenoid, possibly with an associated sphenethmoid (presphenoid), is surely present internal to the epipterygoids, but I have not attempted to develop this area of the skull. Behind their point of ventral emergence, the conjoined parasphenoid and basisphenoid expand into a roughly triangular area, with raised edges and an essentially flat ventral surface carrying a medial ridge. The anterior portion of this surface is obviously the basisphenoid, covered ventrally by the parasphenoid; the posterior portion is part of the occipital complex, but the suture between the two is generally obscure. On either side of this area is a large jugular foramen, facing ventrally, and presumably carrying nerves IX-XI. I have no certain evidence of hypoglossal foramina. Beyond the lateral rim of the jugular foramen, there is a sharp shift to a laterally facing surface where there is a well-developed fenestra ovalis. I am uncertain as to the sutural relations of the opening. Its anteroventral boundary appears to be formed by the parasphenoid-basisphenoid. In well-preserved specimens, the remainder of the fenestra is bounded by a continuous raised ring of bone, not subdivided, which is separated from the adjacent regions of the otico-occipital complex by distinct grooves. Anterior to the fenestra is the foramen for nerve VII.

Posterolateral to the fenestra ovalis, there stretches the stout paroccipital process of the opisthotic. Laterally it ends bluntly. It

is here buttressed by the squamosal but the tip of the process is unossified; presumably there was some degree of kineticism here. As noted above, the posttemporal fenestra passes forward above the paroccipital process, to emerge anteriorly in a gap between the squamosal and the more anterior, prootic, aspect of the otic capsule. Ventroanteriorly, the paroccipital process thins; at its outer edge it extends downward and forward to reach the posterior end of the quadrate ramus of the epipterygoid. Continuous with the paroccipital process, there is seen on the lateral surface of the braincase (as on the ventral aspect) a forward extension of the otic capsule, the prootic region. Its thin anteroventral margin passes forward and medially to form the upper boundary of the pterygo-paroccipital foramen and then meets, or is covered by, the lateral extension of the parasphenoid. Laterally, the prootic is widely exposed. Dorsally and posteriorly, it is separated from the parietal and squamosal, as noted earlier, by a venous channel; anteriorly, it is in contact with the posterior margin of the broad laterally-facing plate of the epipterygoid; ventrally, it continues in contact with the epipterygoid until the pterygo-paroccipital foramen is reached.

LOWER JAW

(Figs. 6-7)

The lower jaws are present in three specimens. In all three the posterior tip is imperfect. The jaw is of the type characteristic of advanced cynodonts generally. The dentary is dominant, extending almost the entire length of the ramus. It forms nearly all of the strong backward-slanting symphysis. The dentary portion of the lower margin of the ramus is essentially straight. Posteriorly, it terminates at a sharp right angle, as in certain other advanced forms; from this point the ventral boundary of the dentary turns sharply upward and then turns backward with a somewhat thickened lower margin. There is a highly developed ascending ramus, which dorsally curves backward at a moderately sharp angle; thence the boundary curves forward, downward, and backward to terminate just above, and external to, the articular region. It is reasonable to believe that the posterior tip of the dentary was concerned, together with the articular, in jaw articulation.

On the inner surface of the dentary, a sharp ridge extends forward from the posterior tip of the bone, below which the bone is excavated for the reception of posterior elements of the jaw; more

anteriorly, the inner surface is grooved for a narrow meckelian canal which extends from a point just behind the symphysis back to a point where it is covered by the prearticular. Below, and partially covering this meckelian groove, is a thin and narrow splenial, which takes a minor part in the symphysis and extends backward to a point on the posterior margin of the dentary above its angular process.

Of other elements of the "normal" reptilian internal surface of the jaw, there is, in the material, little positive evidence of the coronoid, which was presumably present in life as a thin flake of bone on the inner surface of the dentary in the region of the base

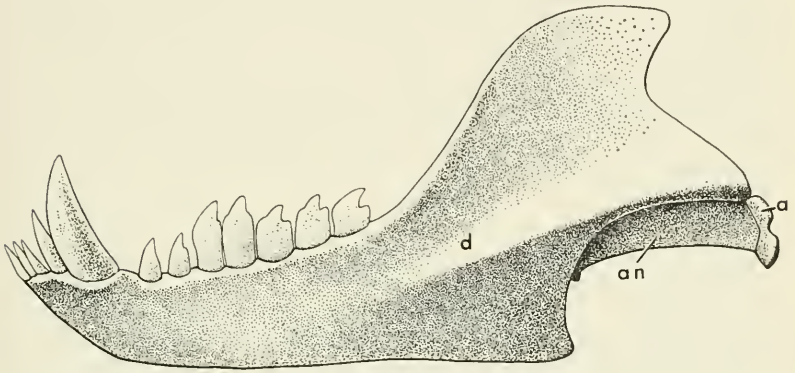

Fig. 6. Lateral view of the lower jaw of *Probelesodon lewisi.*

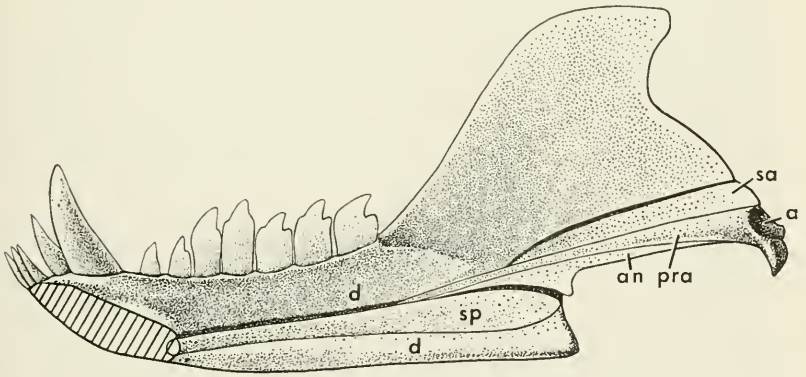

Fig. 7. Medial aspect of the lower jaw of *Probelesodon lewisi.*

of the ascending ramus. Below the assumed position of the coronoid is the slender anterior end of the prearticular, which extends backward, gradually widening, to fuse with the articular. The surangular is completely covered externally by the dentary. In the type, the bone is absent, but its position is obvious because there exists a deep channel for its reception on the inner surface of the dentary; in a second specimen, the bone is present but cannot be completely seen. The angular has a modest external exposure. Internally, the angular is completely covered posteriorly by the prearticular; more anteriorly, there is a narrow exposure of the bone below the prearticular, dwindling to a point anteriorly. Ventrally, just anterior to the point where the dentary covers the bone externally, a small ventral prong is the last remnant of the reflected lamina of the angular, so prominent in the therapsid ancestors. At the posterior end of the jaw, fused to the prearticular, is the articular, essentially an oval structure presenting an articular cup facing posterodorsally, and with a modestly developed retroarticular process.

DENTITION

The dentition is of an orthodox cynodont type. There are four upper incisors in each premaxilla, cylindrical, long, and slender, and set close together in a somewhat arched transverse row; they are slanted strongly backward below the pointed snout. Below, on each side, are three similar incisors directed forward as well as upward. There are well-developed canines both above and below, sharply pointed and slightly recurved; the upper ones are somewhat the stronger. In the holotype, the canines are in process of replacement. Several of the larger specimens have nine upper cheek teeth; the holotype, presumably somewhat immature, has eight, with a ninth erupting posteriorly on one side; an "infantile" specimen has eight. The lower cheek teeth are well seen only in the holotype and in an "infant." In the better preserved of the two rami of the type, there are seven teeth, with, apparently, an eighth developing posteriorly. In the "infant," the lower dentition is not too well preserved, but only six cheek teeth are seen.

The cheek teeth have single roots which are not deep, as witnessed by the fact that in the fossil specimens, they are frequently displaced or lost. (In the related *Belesodon,* for example, all teeth had been lost in the two known specimens, so that one was not even sure whether one was dealing with a carnivore or a gomphodont; in several of the specimens of the Chañares form, a

considerable portion of the cheek teeth had been lost before burial.) The teeth are of a common cynodont type, laterally compressed, sharply pointed, and with a tendency for the development of a fore-and-aft cusp row. As in a number of thrinaxodontids and related chiniquodontids, there is a strong trend for a backward curvature of the major cusp. There is some individual variation, but, in general, in the first two upper teeth — and sometimes in the third as well — there is only a single cusp, curved backward to a slight degree. Back of this, in the upper jaw, there is an increasing development of a posterior accessory cusp, associated with a fore-and-aft lengthening of the tooth. In the only good specimen available of the lower jaw dentition, the development of the posterior cusp is initiated on the second tooth present. In the upper jaw, there tends to be a development of a small anterior cusp, somewhat toward the inner surface. In the one well-preserved lower jaw ramus, an anterior cusp is present on teeth four to six.

I have seen no tendency for the development of accessory "cingulum" cusps, such as might be expected in forms related to mammal ancestry.

THE FAMILY CHINIQUODONTIDAE

In 1956 Watson and I arranged the carnivorous cynodonts in three families in morphologically progressive order — Procynosuchidae, Thrinaxodontidae, Cynognathidae. At that time, we included the then-known chiniquodontids in the Cynognathidae, since they were obviously more advanced than the thrinaxodonts in such characters as the development of a free angle of the dentary. In 1956 Huene erected the family Chiniquodontidae for *Belesodon* and *Chiniquodon,* but gave no definition. These two forms (particularly *Chiniquodon*) were then very poorly known; I have elsewhere (1969) given additional data on these two genera which show that they, plus *Probelesodon,* form a natural group, clearly distinct from the Cynognathidae and that they deserve, as Huene felt, segregation as a separate family of advanced cynodonts. They share with the better known advanced cynodonts such features as the great development of the dentary and corresponding reduction of the other jaw elements. But there are notable differences from the cynognathid condition. For example, they lack the broad posterior connection of zygomatic arch and occipital crest seen in cynognathids, and have retained a more primitive situation here. Again, they lack the longer snout

and proportionately narrow skull of typical cynognathids, and preserve the shorter snout and very broad zygomatic region seen in thrinaxodontids. It is probable that for chiniquodontid ancestry we must look to a descent from thrinaxodontids parallel to that of the cynognathids. *Sinognathus* (Young, 1959), from the early Triassic of China, may be antecedent, although the palate is less developed.

The unique chiniquodontid feature, never attained by known cynognathids or thrinaxodontids, is the remarkable elongation of the secondary palate. This is a very advanced character unrivalled in any other described therapsids, and paralleling the mammalian condition. We have noted above the fact that the dentary is close to, if not actually in contact with, the squamosal; but neither in the present genus nor in the Santa Maria chiniquodonts is there any development of special squamosal-dentary articular surfaces. In described chiniquodonts, as in cynodonts generally, there remains a large unossified area in the braincase wall, to be filled in by orbitosphenoid-presphenoid development before a mammalian condition is reached. *Probelesodon* and its allies may be close to the line of ascent toward mammals, but there is still a considerable distance to go.

CYNODONT ANCESTRY

Above, we discussed the relationship of *Probelesodon* to other cynodonts. It may not be amiss to discuss in addition the unsettled question of the ancestry of the Cynodontia as a whole.

In 1956 Watson and I proposed that the therapsids be grouped in two large suborders, the Theriodontia and Anomodontia — the former term covering the main carnivore groups, such as the Gorgonopsia, Cynodontia, Therocephalia, and Bauriamorpha; the latter term, used in a broad sense, for the herbivores — the herbivorous Dinocephalia, Dromasauria, and Dicynodontia. This proposal appeared eminently reasonable and has, I believe, been rather generally accepted in most regards. However, some years ago (1961) I pointed out one shift which seemed necessary. It seems certain that the ancestral therapsids, of sphenacodont descent, were carnivores, and hence Watson and I included in the Theriodontia the earliest and most primitive carnivorous therapsid group then recognized, the Titanosuchia or carnivorous Dinocephalia. But study shows that nearly all the forms usually included in the Titanosuchia possess the peculiarly "shouldered" anterior teeth found in the herbivorous Dinocephalia. It thus

appears that, with this specialization already developed, the titanosuchians cannot be placed in the Theriodontia as a basal therapsid group but must instead be considered as ancestral anomodonts. Where, then, shall we find truly ancestral therapsids? Such types known to me in 1961 included only *Phthinosuchus* and a few other poorly known forms from the early Middle Permian of Russia. In skull structure, *Phthinosuchus* had attained therapsid status, but barely so, and is in many regards closely comparable to the ancestral sphenacodonts. I therefore erected for this genus and its relatives the suborder Phthinosuchia as a basal therapsid stock potentially ancestral to such theriodont groups as the Therocephalia, Gorgonopsia, and Cynodontia, and ancestral, through the Titanosuchia, to the Anomodontia as well.

At about this time Boonstra, whose work has been concentrated in great measure on the reptiles of the Tapinocephalus Zone of South Africa, visited Moscow, familiarized himself with the Middle Permian faunas of Russia, and, on his return home, published (1963) an excellent paper on the early phylogeny of therapsids. Although my work of 1961 was not known to him when he wrote, he had come to very much the same conclusions that I had as regards the interrelationships of early therapsids. He recognized the truly primitive position of *Phthinosuchus* and its relatives, and erected a separate basal group for them. His attention, however, was concentrated not so much on *Phthinosuchus* as on *Eotitanosuchus* (Chudinov, 1960), description of which was not yet available when my 1961 paper was prepared, and he hence used the term Eotitanosuchia rather than Phthinosuchia.

It seems certain, then, that the Cynodontia are of ultimate phthinosuchian (or eotitanosuchian) derivation. But were they directly derived, or is their descent to be traced through one or another of the familiar theriodont groups? In earlier decades, the Gorgonopsia were rather generally thought to be cynodont ancestors. Such ancestry was long favored by Watson (1920, 1951). In a number of regards, the gorgonopsians represent a primitive morphological stage antecedent to that of the cynodonts (and, as a minor point, are the only therapsid group apart from the cynodonts in which the primitive 2.3.4.5.3 phalangeal formula is known to have been retained). But there are few indications among gorgonopsians of any trend toward a cynodont condition; the gorgonopsians seem to have been, so to speak, "frozen" in a primitive theriodont morphological pattern, and, in addition, universally retain such gorgonopsian "trademarks" as the preparietal bone and a reduced cheek tooth series.

If the gorgonopsians are excluded, where can we turn? In recent decades the Therocephalia, or rather that advanced series of therocephalians termed the "scaloposauroids" (which Watson and I preferred to group with their Triassic descendants, the Bauriamorpha), have been favored as cynodont ancestors. The scaloposauroids show various advanced characters. The skull is lightly built, there is a trend toward a secondary palate, the dentary is well developed, and so on. These trends lead toward the advanced condition seen in *Bauria;* but, it has been suggested, may there not have been a second advanced line leading to the cynodonts? To be sure, most scaloposauroids tend to be long-snouted forms with a long tooth row, with, in general, little differentiation of canines, and with the characteristic therocephalian-bauriamorphan "trademark" of large palatal vacuities. However, reversal in such features might have occurred and if transitional forms were to be found, belief in a scaloposauroid ancestry of the cynodonts would attain credibility.

Broom, although early disposed to a gorgonopsian ancestry, later (1938) inclined toward a therocephalian origin. Brink has been a recent major advocate of cynodont descent from therocephalians, specifically the scaloposauroids (Brink, 1950, 1951).[1] Since Brink is the only writer who has attempted to give broad consideration to the theory of therocephalian ancestry of cynodonts, his arguments deserve careful consideration.

Brink's attention was attracted to some small skulls named *Silphedestes* and *Silphedocynodon,* which are in general scaloposaurid in type, but in which postorbital and zygomatic arches are absent. Whether this absence in the skulls as preserved is due to their absence in life or to post-mortem damage is not certain. The presumed absence of arches has, of course, no bearing on possible cynodont relationships, since these arches (slender in scaloposaurids) are highly developed in cynodonts. Brink (1951: 340) considered that *Silphedestes* (as well as *Silphedocynodon*) was "truly a cynodontid therocephalian, to be more cynodont than therocephalian and that it should be grouped rather under the Cynodontia than under the Therocephalia."

[1] Unlike Watson and myself, Brink considers the scaloposaurs to pertain to the Therocephalia proper rather than to the Bauriamorpha. In this section I have followed him in using "scaloposaur" and "therocephalian" interchangeably for the presumed scaloposaurid ancestors of the cynodonts.

In the papers cited above, Brink failed to give specific reasons for assuming the relationship of cynodonts to these forms (or to scaloposauroids in general). A further specimen, which Brink believed strongly confirmed his belief in the scaloposauroid origin of the cynodonts, was a small skull from the Cistecephalus Zone, which he prepared by the grinding method and reconstructed, and named *Scalopocynodon* (Brink, 1961). It had been damaged posteriorly before burial. Here, as in the silphedestids, zygomatic and postorbital arches are absent, but again, whether this is a natural condition or is due to pre-burial damage is uncertain. The animal is definitely and clearly a cynodont, as Brink agrees, although a cynodont of a primitive sort. It is closely comparable to the procynosuchid cynodonts and differs markedly from scaloposauroids in numerous regards, such as the secondary palate, the dentition with cusped "molars" and highly developed canines, broad alisphenoids, absence of the large palatal fenestrae of scaloposauroids, a cynodont double condyle, and so forth.

On the other hand, Brink lists 17 features which he believes to indicate the relationship of *Scalopocynodon* to the Therocephalia. I shall consider these 17 points in some detail, using Brink's numeration.

Several points may be immediately ruled out. The absence of postorbital and zygomatic arches (2, 3) and the "feeble structure" of the posterior ends of the squamosals (11), if "natural," are suggestive of scaloposauroids, particularly the supposedly archless silphedestids. However, this has nothing to do with cynodonts, in which stout arches are universally present. Cited as a potential scaloposauroid character is the possible entrance of the frontals into the orbital margin (17); however, conditions here are uncertain.

Cited as further evidence for scaloposauroid relationships are various primitive features lost or modified in typical cynodonts but retained in therocephalians and bauriamorphs. These include:

(1, 5, 7). The presence of an interpterygoid vacuity and the consequent similarity of the pterygoids of the specimen to those of therocephalians (p. 144). No interpterygoid vacuity is present in advanced cynodonts, where pterygoids are firmly fused to the basicranial axis; such vacuities are present, however, not merely in scaloposauroids but in all primitive therapsids. The contrast of the parasphenoidal keel and rostrum to those of cynodonts is, of course, due to the fact that the parasphenoid-basisphenoid is, primitively, still free from the pterygoids, rather than fused into the basicranial bar.

(4). In contrast to cynodonts, and like scaloposauroids, the pterygoids are tooth-bearing. This is merely a primitive character, retained in titanosuchians and gorgonopsians as well as therocephalians.

(6). "The transverse bones contribute rather substantially to the pterygoid processes." This is a general primitive therapsid feature. The area of the "transverse" (ectopterygoid) in the specimen being considered is about the same as in, for example, the titanosuchian *Titanophoneus* and the gorgonopsian *Saurictonus* (Romer, 1961, fig. 11).

(9). The posterior face of the skull had undergone damage before burial and is not figured by Brink. He states, however, that it is therocephalian-like in the shallowness of the occiput and in the fact that the occipital crests are low and not very sharp. This, however, is a generally primitive character; the impression I get from his description is that of, for example, Efremov's figure (1954, fig. 51) of *Phthinosuchus*.

(12). "The parietal region is not sharply crested." This is merely a primitive feature (cf. for example, *Phthinosuchus* [Efremov, fig. 49]).

(13). "The pineal is situated far back." It does not appear to be particularly far back, but a posterior position is a primitive synapsid feature (cf. *Phthinosuchus*, Efremov, fig. 49).

(15, 16). The prefrontals extend well forward and laterally, preventing a lacrimal-nasal contact. Such a contact, seen in cynodonts, is unique among theriodonts; its absence is primitive, not an exclusive therocephalian feature.

Apart from this series of primitive characters retained in *Scalopocynodon* as well as in scaloposauroids, there are three further points mentioned by Brink as supporting therocephalian relationship which are of dubious importance. (8). The sella turcica is shallow in *Scalopocynodon*, and where known in cynodonts is better developed. However, this region is known in but few therapsids, and the significance of variance here is obscure.

(10). One paroccipital process is preserved in Brink's skull; he states that it is shorter and slenderer than that of cynodonts. It appears to be rather shorter proportionately than in cynognathids, but it does not appear to differ notably from the paroccipital process in other cynodonts for which I have available material or illustrations.

(14). Brink agrees that the alisphenoid (epipterygoid) is as broadly developed as in typical cynodonts but without as much overlap of the prootic, and further, the bone is not as high as is

proper in cynodonts. However, the difference in prootic overlap does not appear great, and I see no appreciable difference in alisphenoid height between *Scalopocynodon* and typical cynodonts.

To sum up, such a primitive cynodont as *Scalopocynodon* shows a number of archaic therapsid characters also retained in scaloposauroids. But I fail to see that *Scalopocynodon* furnishes the slightest evidence that scaloposauroids have anything to do with cynodont origins. I find it difficult to believe that long-snouted scaloposaurs with a nearly homodont dentition, large palatal vacuities and, as far as known, a reduced phalangeal formula of 2.3.3.3.3, should rapidly reverse their evolutionary trends, re-acquire stout canines, close their palatal vacuities,[1] re-acquire lost phalanges, and rather abruptly take on various other cynodont characters. It is much more reasonable to believe that the cynodonts evolved directly from primitive therapsids of the *Phthinosuchus-Eotitanosuchus* type without any close affiliation with other theriodont groups. The only argument against such a belief is the negative one that no pre-cynodonts are known from the Tapinocephalus and Endothiodon zones. Possibly the ancestral forms were rare or possibly they were absent from the Karroo before Cistecephalous Zone times — at which time we know that communications between South Africa and Eurasia were open, and that primitive cynodonts were already present in the pre-Ural region of Russia.

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POSTLARVAL *SUDIS* (PISCES: PARALEPIDIDAE) IN THE ATLANTIC OCEAN*

David L. Shores

ABSTRACT. The paralepidids, *Sudis atrox Rofen* 1963 and *Sudis hyalina* Rafinesque 1810, are present in midwater collections from the Atlantic Ocean. Postlarval development is described and illustrated with particular attention given to head spination. This character is similarly developed in both species, but it differs in form and degree of head coverage (more extensive in *S. atrox*) providing a basis for species differentiation.

INTRODUCTION

The WHOI midwater trawl collections (Fig. 1) contain numerous postlarval paralepidids referable to the genus *Sudis*. Examination of these shows that two species are represented. One, *Sudis hyalina* Rafinesque 1810, has been known only from the North Atlantic and the Mediterranean. The other, referable to *Sudis atrox* Rofen 1963, has been known only from the North Pacific. This note describes the postlarval development of *S. atrox,* compares this development with that of *S. hyalina,* and records the Atlantic distribution of these species.

STUDY MATERIAL

The study material consists of 132 specimens of *S. atrox* and 32 specimens of *S. hyalina*. Collection data is shown in Tables 1 and 2 with the distribution of catches plotted in Figure 1. The specimens were caught by midwater trawls with no opening-closing mechanism. The majority of the specimens (153 out of 164) came from tows shallower than 250 meters and show that the two species can be expected in any collection at this depth or shallower.

* Contribution No. 2319 from the Woods Hole Oceanographic Institution.

Accordingly, the "no catch" records in Figure 1 (squares) show the distribution of tows that were at appropriate depths for catching the two species but which nevertheless took no specimens. Figure 1 shows that *S. hyalina* is a northern species and *S. atrox* is a tropical one, with the two occurring together in the Gulf of Mexico. *S. hyalina* has also been found in our collections from off the Rio de la Plata (ca. 32°S) and thus a biantitropical distribution is suggested. The two specimens of *S. atrox* collected near 38°N, 67°W are probably Gulf Stream waifs.

Sudis atrox was described by Rofen (1963) from a 75 mm SL Pacific Ocean specimen taken from the stomach of *Alepisaurus*

Figure 1. Atlantic distribution of *Sudis atrox* Rofen and *Sudis hyalina* Rafinesque, based on captures listed in Tables 1 and 2. "No catch" records are all trawls shallower than 250 m that did not take specimens.

caught on longline gear at 29°26′N, 134°59′W. Pacific postlarval specimens were reported by Berry and Perkins (1966) with a drawing of a 21.5 mm SL specimen. The adult specimens of the two species differ by vertebral counts (59-60 for *S. hyalina* vs. 53-54 for *S. atrox*) and by the number of lateral line pores (four to seven per each lateral line section for *S. hyalina* and three for *S. atrox*) (Rofen, 1966). My specimens have been identified by vertebral counts obtained from X-rays of representative specimens (60-61 vertebrae for five *S. hyalina* and 52-54 for 15 *S. atrox*) and by the postlarval characters of pigment patterns, degree and type of spination, and pectoral fin length.

DEVELOPMENTAL CHARACTERS

SUDIS ATROX

The development of *S. atrox* closely resembles that of its congener, *S. hyalina*. The pectoral fins are long and spines are present on the head. The *S. atrox* head spination is so extensive in development and unique in form that it can be used to identify postlarval specimens. The spines are located on the head as follows:

Preoperculum. Large, obvious spine at the posteroventral angle, with serrated edges and hooked processes along its length. Two large processes at its base, one directed posterodorsally and the other ventrally. Ventral and posterior edges of the preoperculum with spine-tipped scalloped flanges. Ventral flange obvious; posterior one small and inconspicuous.

Dorsal surface of head. Two spine-tipped scalloped flanges above eye, a shorter one directed laterally and a longer one directed dorsally. Paired spine-tipped scalloped flanges medial to supraocular flanges on dorsal surface of head from tip of snout posteriorly to a line between anterior margins of orbits.

Mandible. Spine-tipped scalloped flange along side of lower jaw.

Shoulder. Two spines.

These spiny processes are observed in the smallest specimen (5.5 mm SL) and are most extensively developed in the 10 to 20 mm specimens. They are worn down and indistinct in specimens larger than 30 mm (Table 3).

The development of *Sudis atrox* is also distinguished by six peritoneal sections, by the late development of the elongated pectoral fin, and by the early development of widespread trunk pigment.

5.5 mm SL (Fig. 2A). Head deep, top involuted with a ridge on each side. Ridge with a conspicuous spine-tipped scalloped

flange. Spiny flange along ventral edge of preoperculum and three relatively large spines at the posteroventral preopercular angle. The middle one of these three spines, which points posteroventrally, is truncated. It is apparently broken off; another specimen of approximately the same size (6.0 mm SL RHB 1717) has this middle spine longer and stouter than the other two with an

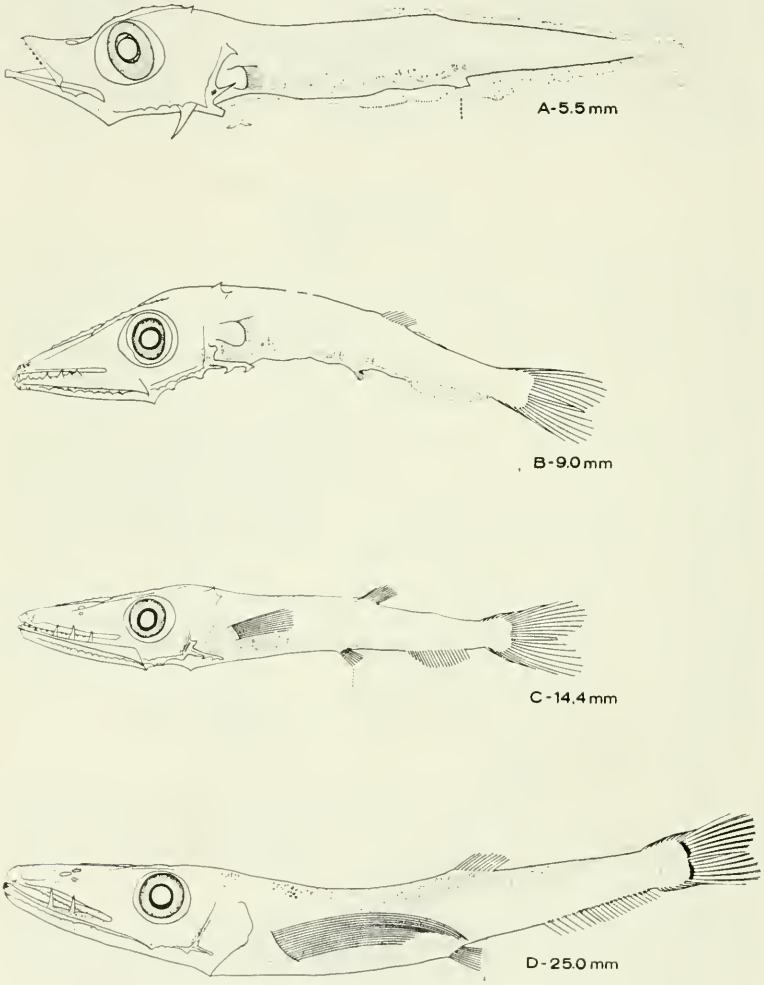

Figure 2. Postlarval stages of *Sudis atrox* Rofen. A. RHB 1107. B. RHB 1291. C. RHB 1108. D. RHB 1294. Drawn by Martha Howbert.

antrorse hook ventrally located near the spine tip (shown in Fig. 2A in broken line). Eye compressed, obliquely oriented. Pectoral fin rounded, short, on short stalked base; rays evident. Dorsal and anal fin bases barely discernible in embryonic finfold. Peritoneal pigment extending two-thirds length of trunk from pectoral base to a point over anterior section of rudimentary anal fin. Anterior half of this pigment diffuse; posterior half partitioned into three sections. Dense cluster of small pigment cells on base of preoperculum angle spine.

9.0 mm SL (Fig. 2B). Head deep, massive, flat on top, sharply angular between top and sides. Snout length and head length relatively longer than in 5.5 mm specimen (50.0% vs. 38.0% for snout length and 46.6% vs. 32.0% for head length). Four canine teeth on lower jaw. Head studded with spine-tipped scalloped flanges that are well developed along top of snout, over eye (two flanges here — one directed laterally and one directed dorsally), along lower jaw, and on preoperculum ventral edge. Also a large spine extending back from posteroventral angle of preoperculum, with serrated upper and lower edges and two prominent antrorse hooks (Fig. 4A). This spine has a triangular cross section large at base and decreasing in size out to tip, with the two antrorse hooks stemming from laterally directed apex or 'keel' of this triangular cross section.

Fins well formed with interspinous rays. Pectoral fins short, extending only one third of distance to ventral fin base. Six well formed peritoneal sections going back to anal fin origin. Pigment patches at jaw tips, scattered cells on lower jaw, small ones on preoperculum posterior margin and two large stellate chromatophores on base of preopercular angle spine. Large chromatophores spread evenly over cerebral hemispheres, one of the same over hind brain, and several between the two brain sections.

14.4 mm SL (Fig. 2C). Head form as in 9.0 mm specimen. Three canines on left side and four on right. Pectoral fins reaching halfway to ventral bases. Dorsal and anal fins with 10 and 20 rays, respectively. Spines about head as in 9.0 mm specimen, excepting more spine tips in the flanges (Table 3) and two obvious spines added to preoperculum ventral edge, apart from spiny flange already described for that area. Spine deterioration indicated in dorsally directed supraocular flange in which spine tips are relatively blunt. Spine deterioration suggested in preopercular angle spine in which the hooks are smaller in relation to the total size of this spine than is observed in 9.0 mm specimen.

Pigment about head as in 9.0 mm specimen, excepting thicker coverage of large chromatophores over brain, with dense arc of same over anterior edges of cerebral hemispheres. Trunk with broad grouping of large stellate chromatophores on dorsum between nape and dorsal fin origin, patch of chromatophores at dorsal origin, and grouping of three pigment cells over hypural plate. Six peritoneal sections.

25.0 mm SL (Fig. 2D). General body form essentially as before with large deep head on relatively short body. Three canines left and four right. Pectoral fins long, reaching beyond ventral bases; 15 rays. Pigment cells proximally and medially on rays 1 and 2; patches medially and distally on rays 3-7. Other fin ray counts: Dorsal — 10; Anal — 21; Ventrals — 9.

Head spination not apparent. Spines in scalloped flanges fewer (Table 3). Spines, when present, worn down as in supraocular flanges, where eight spines in lateral flange and thirteen spines in dorsal flange are reduced to rounded irregularities in what appear to be only eroded or broken ridges over eye.

Body pigment extensive, evenly spread on dorsum and sides of same spread over hypural plate. Anterior portion of lateral line ventrally edged with small pigment cells. (Lateral line not pigmented.) Fin bases with varying degrees of pigmentation: large light chromatophores on roots of dorsal and anal fins; small dark cells at base of ventral rays; and large, moderately dark pigment cells forming vertical line at base of caudal fin. Six peritoneal sections.

38.0 mm SL (Not figured; RHB 1281). Head and body essentially as before. Head deep, massive. Four canines. Pectoral fin broken off; 15 rays. Dorsal — 12 rays; Anal — 21 rays; Ventrals — 9 rays. Vestiges of post larval spination present but very small and obscure. Primary character is trunk pigment, which is denser and slightly more extensive than in 25.0 mm specimen. Lower margin of lateral line pigmented for entire length (no pigment over lateral line). Vertical bar at caudal base darker, more apparent. Six peritoneal sections.

Sudis Hyalina

The development of *S. hyalina* closely parallels that of *S. atrox*. The body form is essentially the same, with a relatively short body and a large head. Spines are present over the eye and on the preoperculum lower margin.

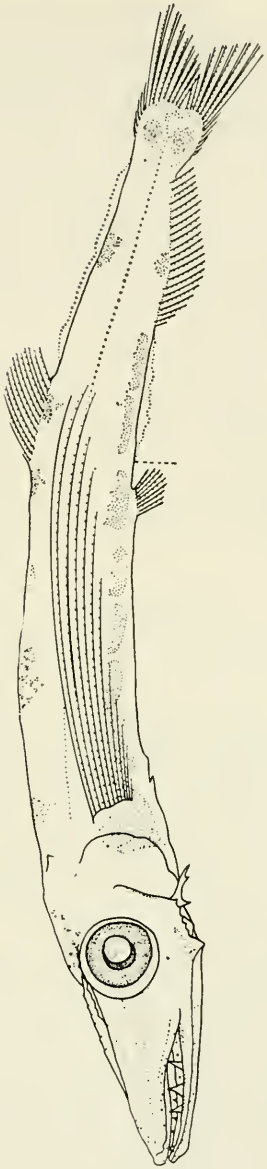

Figure 3. Postlarval *Sudis hyalina* Rafinesque, 16.1 mm SL, RHB 1307. Drawn by Martha Howbert.

16.1 mm SL (Fig. 3). Head large (31.6% of SL) but not as deep and massive as in *S. atrox*. Trunk short but not as deep and stout appearing as in *S. atrox*. Pectoral fin very long, extending beyond ventral bases and anus; small pigment cells near bases of first five rays, larger blotchy cells further out on rays 2-7.

Spination includes eight spine tips on scalloped flange over eye, six very small spine tips on posterior half of flange running length of snout, five spine tips on scalloped flange along preoperculum ventral edge, and a relatively large spine extending posteriorly from posteroventral angle of preoperculum (Fig. 4B). This latter spine has a retrorse hook distally (giving spine a bifurcated appearance) and a second larger retrorse hook at base.

Trunk pigment concentrated in patches, with six patches on dorsum (three anterior to dorsal fin, one at dorsal origin, one at dorsal base, and one posterior to dorsal base), one patch midway on anal fin base, and two over hypural plate above and below notochord. Eight peritoneal sections. Large stellate chromatophores over brain. Small pigment cells on jaws and margins of preoperculum.

COMPARISON

The distinctive characters of *S. atrox* are pointed out with reference to *S. hyalina*.

1. *Spination.* Spine-tipped flanges present on both *S. atrox* and *S. hyalina* on preoperculum ventral edge, over eye, and along posterior part of snout. Additional distinctive spines present on *S. atrox* along lower jaw, anterior part of snout flange, and in a second spiny flange over eye. The large spine at preopercular angle in *S. atrox* is distinctive for its serrated edges and one or more antrorse hooks, whereas this spine in *S. hyalina* is smooth with only one retrorse hook (Fig. 4).

2. *Pectoral fin.* Short in early postlarval *S. atrox,* reaching ventral origin in three specimens at 16.5 mm (RHB 1289), 17.3 mm (RHB 1297), and 19.5 mm (RHB 1281). In contrast, the pectoral fin of *S. hyalina* is long, very early in development reaching ventral origin in an 8.0 mm specimen (RHB 1043) and extending beyond ventral base and anus in a 9.0 mm specimen (RHB 1047).

3. *Pigment.* Six peritoneal sections in *S. atrox* vs. seven to eight in *S. hyalina.* Trunk pigment in *S. atrox* evenly spread over trunk surface vs. patch pattern distribution in *S. hyalina.* 14.4 mm *S. atrox* (described in text) — pigment grouping covering middle

half of nape to dorsal fin area, plus pigment patch at dorsal fin origin and three small chromatophores over hypural plate. 16.0 mm *S. atrox* (RHB 1277) — uniform coverage of dorsum back to point halfway between dorsal fin and procurrent caudal rays

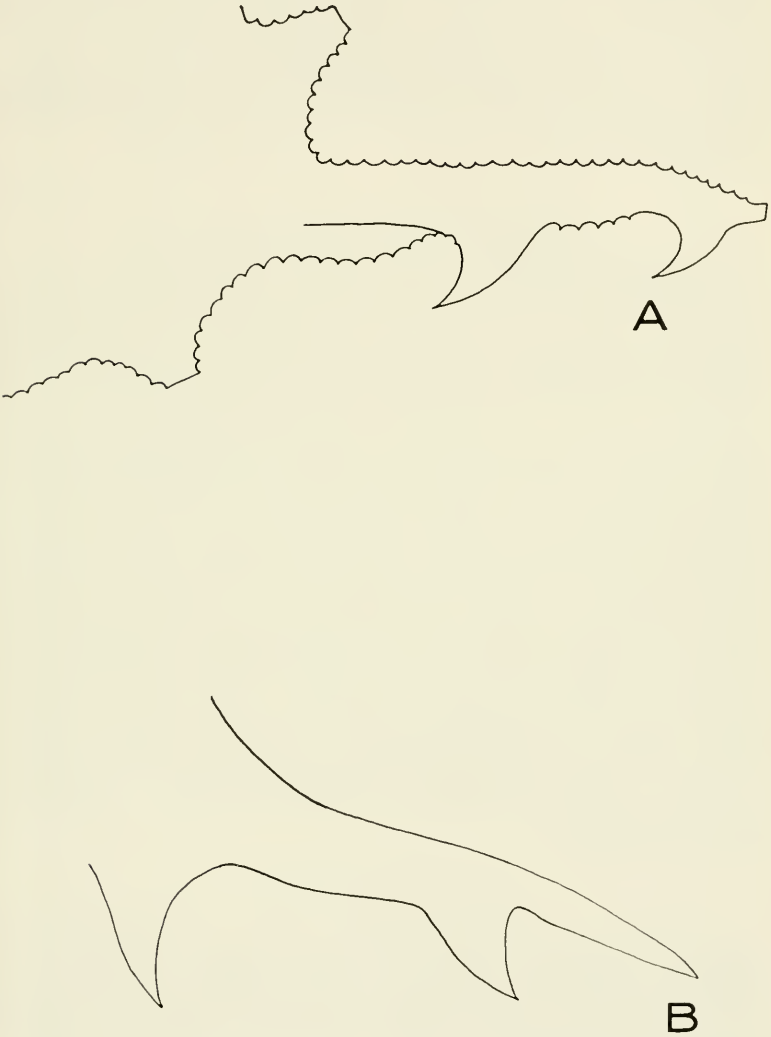

Figure 4. Preopercular spines. A. *Sudis atrox* Rofen, 9.0 mm SL, RHB 1291. B. *Sudis hyalina* Rafinesque, 16.1 mm SL, RHB 1307. Drawn by Martha Howbert.

plus hypural pigment. 19.5 mm *S. atrox* (RHB 1281) — even coverage of dorsum back to procurrent caudal rays all but connected to and continuous with hypural pigment. (See also pigment coverage in 25.0 mm *S. atrox,* Fig. 2D.) In contrast, *S. hyalina* trunk pigment concentrated in nine patches in specimens from 16.1 mm SL (See specimen described and figured above.) to 36 mm SL. Patches clearly defined in 28 mm specimen (RHB 1307), spread out but still recognizable in 33 mm specimen (RHB 1439), and all but blended into uniform coverage in 36 mm specimen (RHB 1313).

RELATION OF *SUDIS* TO MAN

Bites on polypropylene mooring cables serious enough to sever the individual fibers have been reported off Bermuda and were connected with fish through tooth fragments left on the cable (Turner and Prindle, 1965). *Sudis hyalina* has been identified as the fish responsible for certain bites in depths of 600 to 800 meters (Haedrich, 1965). The bites have occurred in pairs on one side of the cable only and presumably have been made by the long canine teeth on either side of the lower jaw. The distance between cuts of a pair range from 30 to 60 mm. Reference to the tooth arrangement of a 405 mm *S. hyalina* with an 18 mm distance between dentaries places the size of the cable-biting *Sudis* at more than a meter in length. These bites might just as well have been caused by *S. atrox* as by *S. hyalina.* The mandibular canine teeth of both species are long and strong. The fragments in the rope have serrated edges matching the teeth of adult *S. hyalina.* The teeth of the 75 mm juvenile holotype of *S. atrox* have smooth edges (Rofen, 1963) as does a 75 mm specimen of *S. hyalina* (Rofen, 1966). Until teeth of larger specimens of *S. atrox* are obtained, the question of the origin of the bites described by Haedrich (1965) remains unanswered.

ACKNOWLEDGEMENTS

My thanks go to Richard H. Backus, James E. Craddock, and Richard L. Haedrich, Woods Hole Oceanographic Institution, for their encouragement and critical reviews in preparing this paper. The work was supported by NSF Grant GB-7108 (R. H. Backus, principal investigator).

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(Received 20 August 1969.)

TABLE 1 — STUDY MATERIAL

Sudis atrox Rofen, 1963

Coll. No.	*No. of Specs.*	*Size Range (SL) (mm)*	*Position*		*Date*	*Max. Depth (m)*
581	1	8	19°21′N,	66°20′W	2 Mar. 54	90
962	1	12	5°24′N,	39°55′W	13 Feb. 63	860
967	1	8	0°26′N,	32°06′W	18 Feb. 63	60
972	3	20-21	0°03′N,	25°00′W	23 Feb. 63	87
981	1	9	5°42′S,	32°25′W	1 Mar. 63	120
1101	2	25-38	13°18′N,	60°05′W	13 June 65	187
1105	1	15	15°42′N,	64°13′W	14 June 65	230
1107	4	6-12	19°52′N,	69°46′W	16 June 65	140
1108	1	14	19°55′N,	70°04′W	16 June 65	525
1200	1	14	16°13′N,	59°09′W	11 Feb. 66	450
1202	4	10-11	13°00′N,	49°38′W	14 Feb. 66	220
1216	1	9	1°12′N,	44°39′W	11 Apr. 66	410
1218	1	21	9°12′N,	47°03′W	16 Apr. 66	360
1222	2	8-22	13°55′N,	57°00′W	30 Apr. 66	300
1253	4	10-17	16°38′N,	64°27′W	25 May 66	133
1258	2	28-35	13°32′N,	71°24′W	27 May 66	210
1261	1	24	13°04′N,	73°12′W	28 May 66	300
1263	3	14-43	12°58′N,	73°34′W	29 May 66	120
1274	8	8-12	13°07′N,	78°23′W	5 June 66	109
1277	21	10-17	16°12′N,	78°00′W	6 June 66	198
1281	2	20-38	17°08′N,	79°35′W	6 June 66	205
1282	5	11-18	17°07′N,	79°32′W	7 June 66	185
1289	4	17-35	21°11′N,	85°12′W	10 June 66	170
1290	2	12-15	21°17′N,	85°22′W	11 June 66	124
1291	2	9-12	22°54′N,	91°36′W	12 June 66	57
1294	3	15-25	20°48′N,	95°48′W	17 June 66	100
1297	13	15-33	23°13′N,	94°50′W	19 June 66	128
1298	3	19-22	23°55′N,	94°00′W	19 June 66	370
1307	1	13	27°01′N,	90°02′W	22 June 66	95
1310	1	14	26°12′N,	87°54′W	23 June 66	2150*
1423	1	29	12°21′S,	31°04′W	1 Mar. 67	90
1425	3	5-10	16°07′S,	29°59′W	3 Mar. 67	85
1427	2	15-18	18°10′S,	29°40′W	5 Mar. 67	140
1428	4	6-8	18°21′S,	29°39′W	5 Mar. 67	75
1432	2	10-11	23°08′S,	32°22′W	9 Mar. 67	110
1505	2	10-10	37°40′N,	66°50′W	25 Aug. 67	105
1713	6	8-11	25°06′N,	67°45′W	1 Dec. 68	125
1716	1	15	23°24′N,	67°30′W	1 Dec. 68	140
1717	6	6-10	23°00′N,	67°29′W	2 Dec. 68	30
1718	3	6-28	22°51′N,	67°30′W	2 Dec. 68	210

1727	1	12	26°46′N,	67°32′W	6 Dec. 68	65
1736	1	13	28°35′N,	67°24′W	8 Dec. 68	87
R/V *'Anton Bruun'* Cr. 19						
Sta. 813	1	45	11°06′N,	78°21′W	7 Aug. 66	2250*

*Oblique tow

The specimens in collections 1107 and 1108 were the first Atlantic specimens of *S. atrox* to be reported (Backus et al., 1969).

TABLE 2 — STUDY MATERIAL

Sudis hyalina Rafinesque, 1810

Coll. No.	*No. of Specs.*	*Size Range (SL) (mm)*	*Position*		*Date*	*Max. Depth (m)*
861	1	28	41°40′N,	61°57′W	15 Sept. 62	64
866	1	11	39°20′N,	66°45′W	18 Sept. 62	68
867	2	17-20	39°03′N,	67°18′W	19 Sept. 62	110
1022	1	16	42°35′N,	45°56′W	10 Sept. 64	50
1043	1	8	39°28′N,	31°00′W	25 Sept. 64	35
1047	1	9	39°25′N,	36°56′W	27 Sept. 64	52
1050	1	11	39°31′N,	43°33′W	29 Sept. 64	53
1263	1	16	12°58′N,	73°34′W	29 May 66	120
1290	2	13-14	21°17′N,	85°22′W	11 June 66	124
1307	10	16-48	27°01′N,	90°02′W	22 June 66	95
1313	1	36	23°55′N,	83°12′W	25 June 66	145
1315	1	12	25°46′N,	79°47′W	26 June 66	71
1438	1	30	32°53′S,	46°06′W	16 Mar. 67	110
1439	2	21-33	32°56′S,	46°12′W	16 Mar. 67	40
1508	1	34	36°27′N,	67°18′W	26 Aug. 67	190
1706	1	13	30°10′N,	67°32′W	28 Nov. 68	217
1727	1	7	26°46′N,	67°32′W	6 Dec. 68	65
1737	1	14	28°45′N,	67°26′W	8 Dec. 68	135
'Captain Bill III', Cr. 65-1						
Sta. MWT-1	2	14-18	38°11′N,	69°47′W	11 May 65	90

TABLE 3

Spine development and deterioration; spine counts in postlarval stages of *Sudis atrox*.

Standard Length (SL) (mm)	*Preoperculum*			*Supraocular*		*Snout*	*Lower Jaw*
	Posteroventral Angle	*Ventral Edge*	*Posterior Edge*	*Laterally Directed*	*Dorsally Directed*		
5.5	3 Long Spines	5	1	—	6	—	2
9.0	Keeled, serrated spine with 2 hooks, 2 basal processes	6	5	3	11	9	9
14.4	Keeled, serrated spine with 3 hooks (and base of 4th), 2 basal processes	8	5	9	13	11	13
25.0	Spine relatively small, serrations irregular, stubby bases of 2 hooks, general deterioration	2	3	8 Worn down spine bases	13 Worn down spine bases	5 Worn down spine bases	12 Blunt spines
38.0	Spine worn down, all but absorbed	—	—	Eroded, irregular flange, no spines		—	Flange with no spines

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CAMBRIDGE, MASS. 30 DECEMBER, 1969 NUMBER 335

TWO NEW LATE CRETACEOUS FISHES FROM MONTANA AND WYOMING[1]

Richard Estes

ABSTRACT. Two new fossil fishes from the late Cretaceous Hell Creek Formation of Montana are described, based on disarticulated material. One of these fishes is also present in the late Cretaceous Lance Formation of Wyoming.

Palaeolabrus montanensis, n. sp., is the first North American record of a genus previously recorded only from the late Paleocene or early Eocene Dormaal deposits in Belgium. Originally described as a labrid teleost, new material from the Hell Creek Formation suggests that it may be a specialized amioid holostean. However, premaxillae and vertebrae of teleostean type may be referable to *Palaeolabrus;* if the association is correct, it could possibly be a very primitive teleost.

Coriops annicolus, n. gen., n. sp., is referred to the teleost family Albulidae. Originally known only from the Lance Formation of Wyoming, it is now also recorded from the Hell Creek Formation in Montana.

INTRODUCTION

The disarticulated remains of two distinctive fossil fishes have been obtained from a collection of lower vertebrate fossils from Bug Creek Anthills, McCone County, Montana. The fossils occur in the late Cretaceous Hell Creek Formation (Sloan and Van Valen, 1965).

Casier (1967) described *Palaeolabrus dormaalensis* from the late Paleocene or early Eocene of Belgium, basing his description on what he believed to be pharyngeal tooth plates. These plates are interpreted here as vomers, and similar elements in the Bug Creek Anthills sample are supplemented by a number of other disarticulated elements probably referable to this genus, indicating the presence of *Palaeolabrus* in the Hell Creek Formation.

[1] Fossil vertebrates from the late Cretaceous Hell Creek Formation, Montana: Contribution No. 7.

In 1964, I referred basibranchial and parasphenoid tooth plates from the Lance Formation of Wyoming to an undescribed genus of Albulidae. Subsequent work has revealed the presence of this fish in the Hell Creek Formation of Montana, and study of a related albuloid family, Phyllodontidae (Estes, 1969), indicates that these dentitions are distinctive enough to warrant a name.

Morphological comparisons given below indicate that the two groups of disarticulated elements noted above belong to different taxa. The Lance Formation form, here referred to a new genus *Coriops,* is much rarer at Bug Creek than in the Lance Formation, and is represented by (in general) smaller specimens; conversely, *Palaeolabrus* does not occur in the Lance Formation localities.

ORDER AMIIFORMES?

Family Palaeolabridae, n. fam.

Type species: Palaeolabrus dormaalensis Casier 1967

Palaeolabrus montanensis, n. sp.

Type. MCZ 9343, tooth plate, probably vomerine.

Paratypes. MCZ 9342, vomerine (or anterior dermopalatine?) tooth plates; 9339, 9341, 9344, right dentary fragments; 9380, posterior dermopalatines; 9347, 9352, entopterygoids(?); 9345, 9351, first (symphysial) coronoids; 9348, coronoid fragments; 9452, prearticular; 9346, 9353, right and left premaxillae; 9350, questionably-referred vertebrae.

Type locality. Bug Creek Anthills, west half of section 9, T 22 N, R 17 W, McCone County, Montana; collected by A. D. Lewis and party, 1964.

Etymology. Latin, *montanensis,* from Montana.

Diagnosis. Distinguished from the only other known species, *Palaeolabrus dormaalensis,* from the late Paleocene or early Eocene of Belgium, by its generally larger size and uniformly styliform teeth lacking any development of an apical point.

Description. Presumed vomerine plates subtriangular, entirely covered with styliform crushing teeth ventrally, each with a tiny enameloid tip that is flattened and slightly depressed below the crown surface (Pl. 3d); dorsally, assumed anterior and lateral borders thickened for articulation with (presumably) premaxilla and maxilla or dermopalatine (Pl. 1a-f).

Posterior dermopalatine (ectopterygoid) strongly twisted, widened at anterior end, tapering posteriorly in both known specimens; teeth styliform as on vomers, larger anterolaterally, becoming much

smaller posteromedially; both specimens show extensive wear and both are broken at both anterior and posterior ends (Pl. 1i-j).

Presumed entopterygoids with a single row of marginal (medial) tooth bases; laterally, teeth appear only as scattered, isolated tooth bases except posterolaterally, where they become grouped in region of presumed contact with posterior dermopalatine (ectopterygoid). Dorsally a ridged, flattened surface present for presumed contact with braincase bones; anterior end of bone pointed, rapidly expanding posteriorly to a flat sheet; all specimens broken (Pl. 2a-b).

Anterior coronoid (first or symphysial) with marked symphysial expansion; several rows of styliform teeth like those of above elements present; posterior coronoids with deeply concave articulating surfaces; lingual surface of posterior coronoids uniformly convex and covered with the same styliform teeth as on palatal elements (Pl. 1g-h)

Prearticular represented by only a fragment of the posterior end, showing semilunar border at edge of mandibular fossa, and a small process curving dorsally toward the dentary; teeth as on palatal elements.

Dentary massive, with flattened coronoid articulation surface on medial side, and open area anteriorly for symphysial expansion of first coronoid; a strong angle formed in the dentary about at level of fifteenth tooth; posteriorly, dentary truncate, with a very small opening for vascular and nervous structures; dentary tooth row single, teeth acrodont; only tooth bases preserved, the latter with wrinkled, irregular borders as on palatal elements; MCZ 9344 with nineteen tooth bases in the complete row; ventrally, dentary weakly sculptured anteriorly, prominent sculpture begins at level of angle of dentary; sculpture deeply pitted; laterally, a deep fossa for ligamentary attachment of maxilla present near end of tooth row; a lateral row of sensory canal pores present; tiny "coronoid" process of dentary present behind last tooth in row (Pl. 2d-e, 3a-b).

Referred premaxillae with weak exterior sculpture; anterior end of bone expanded, roughened, flattened medially, and somewhat laterally-directed; on MCZ 9346, twenty tooth bases present in a single row, with one extra medial tooth base anteriorly; on MCZ 9353, two tooth bases present in the medial row; posterior end of premaxilla excavated dorsally, elongated, and tapering to a point posteriorly (Pl. 2c).

Questionably-referred vertebrae deeply amphicoelous; prominent excavations laterally for the arch bases; neural arch processes projecting above centrum (Pl. 3e-f).

Generic reference. Casier (1967) described *Palaeolabrus dormaalensis* from the Dormaal deposits in Belgium, of latest Paleocene or earliest Eocene age. The type specimen is a bone that Casier believed to be of pharyngeal origin; he therefore referred *Palaeolabrus* to the Labridae. The Hell Creek Formation elements are here interpreted as vomers or perhaps anterior dermopalatines (see below), and they closely resemble those of the Belgian form (cf. Pl. 1, a-b and c-f). *P. dormaalensis* is smaller than *P. montanensis,* and its teeth are also more pointed. This may be only a size-related difference not of specific significance, but some Bug Creek specimens almost as small as the Belgian form do not have pointed tooth crowns. The strongly-ridged anterior and assumed lateral borders of these bones are very similar in the two forms and leave little doubt of the proper generic reference of the Montana form.

Association of elements referred to Palaeolabrus montanensis. Association of these presumed vomerine (or anterior dermopalatine) tooth plates with the posterior dermopalatines, coronoids, and prearticular is clear; the teeth on these elements are all of identical styliform appearance, with a small, slightly depressed cap of enameloid material at the tip (Pl. 3d). MCZ 9345, a well-preserved first (symphysial) coronoid, fits the dentary MCZ 9344 almost perfectly; this seems to confirm association of these two bones, as does the similar wrinkled appearance of the tooth bases of both specimens. The wrinkled tooth bases are also present on the premaxillae and presumed entopterygoids.

Affinities of Palaeolabrus. The unquestionable mutual association of the elements referred here to vomers, posterior dermopalatines, and coronoids makes it clear that *Palaeolabrus* does not belong to the advanced teleost family Labridae. The presence of well-developed toothed coronoids and paired vomers precludes inclusion in any known teleost group, although a very primitive teleost might well have them. The general appearance of the dentary itself (discussed further below) and the fact that the actual symphysis lies on the coronoid are conditions suggestive of the amioids, and these similarities are also present in *Amia* itself. In the dentary the general shape, short tooth row, open symphysial region, enclosed sensory canals, and recessed labial notch near the "coronoid process" (to receive the posterior end of the maxilla) are resemblances to amioids, especially the Amiidae. The strong angulation of the dentary is common in short-jawed "holosteans" but is also compatible with the above resemblances to

amiids. Tooth histology of *Palaeolabrus* and its contemporary *Amia fragosa* (also from the Hell Creek Formation; Estes and Berberian, 1969) indicates general similarity. The specializations often occurring in the orthodentine tissues of teleosts are absent; only simple orthodentinal tubules are present.

The bones of the palate also show amioid resemblances. The posterior dermopalatines are relatively much shorter than those of *Amia,* but the curvature, or torsion, and the presence of a strong lateral ridge dorsally, are resemblances to the Recent genus. Some primitive teleosts, such as elopids, also show this condition, however. The presumed entopterygoids resemble those of *Amia* in having a narrow anterior end, and a flattened, ridged area dorsally for attachment of braincase bones (or cartilages). They differ, however, in having only a single, curved, medial row of teeth, whereas the entopterygoids of *Amia* have a large patch or shagreen of teeth on this bone. This tooth patch in *Amia* does, however, have a curved medial row of enlarged teeth that suggests similarity to the Hell Creek form. The presumed entopterygoid may have been, in life, more denticulate in *Palaeolabrus* than it seems, for palatal teeth are often only irregularly fused to the underlying bones in *Amia,* and in macerated specimens a patchy distribution of teeth may result.

The type specimens of the two species of *Palaeolabrus* are clearly paired bones, as Casier (1967) realized. In considering the possibility of an amioid affinity for *Palaeolabrus,* my first interpretation of these bones was that they were a fused group of posterior superior pharyngeal tooth patches like that of *Amia,* which has a similar, subtriangular shape (Nelson, 1969, pl. 82, fig. 1). In *Amia,* however, these patches are formed of a number of discrete, rounded groups of teeth connected by cartilage, and a small, rounded branchial bone with a prominent dorsal process is incorporated into this patch. No such structures or process is suggested in the type elements of *Palaeolabrus.* The dorsal appearance of the tooth plate is smooth, rather like that of the anterior dermopalatines of *Albula.* On the other hand, while the long posterior process of the *Amia* vomer is not present on the presumed vomer of *Palaeolabrus,* the enlarged anterior and presumed lateral ridges of this element are suggestive of the premaxillary and anterior dermopalatine attachment surfaces of the vomer of the Recent genus (Pl. 1c, e). Tentatively, then, this element is considered a vomer, but it could possibly be an anterior dermopalatine.

Several unique characters and some features dissimilar to amiids now require comment. The premaxillae, referred here to *Palaeolabrus* on the basis of similarity of tooth bases to those of the dentary, are completely unlike those of *Amia,* and strongly resemble those of such primitive teleosts as *Elops* and (to lesser degree) *Megalops* in posterior elongation and absence of the enlarged posterodorsal process of this bone that occurs in *Amia* and other "holosteans." An elopid does occur in the Hell Creek Formation and Lance Formation fauna, and is represented by a few scales, vertebrae, dentaries, and fragments of sculptured skull bones. These elements, aside from their sculpture, suggest a *Megalops*-like form (Estes, 1964; Estes, Berberian, and Meszoely, 1969). The dentaries show that this elopid, while not identifiable as to species, was probably prognathous as in other elopids, and that the jaw margins were covered with several rows of teeth unlike those of *Palaeolabrus.* There is little chance, then, that the premaxillae referred here to *Palaeolabrus* belong to this elopid, quite aside from the reasons noted above for associating them with *Palaeolabrus.*

The vertebrae tentatively referred here to *Palaeolabrus* are also unlike those of amiids or most other "holosteans." They most closely resemble teleost vertebrae, although some amioids, e. g. *Oenoscopus* (Saint-Seine, 1949, pl. 18c), have similar centra. Known Bug Creek Anthills teleosts were relatively too small to have vertebrae of the size referred here to *Palaeolabrus.* It is, of course, possible that a large teleost, other than the elopid noted above, is present and is (so far) unrepresented on the basis of cranial elements. An alternative position is that *Palaeolabrus* is like some other advanced "holosteans" in having a number of progressive, teleostean resemblances; *Amia* itself is quite advanced toward the teleostean level. An extension of this view is that *Palaeolabrus* is a very primitive teleost, perhaps at the pholidophoroid level, a suggestion I owe to Colin Patterson (in litt., 1969).

Cretaceous freshwater fishes are poorly known and most of them are represented only by disarticulated elements. Since most of their marine relatives are preserved as articulated, flattened specimens, it is rarely possible to make detailed comparisons of individual cranial elements, and identification of the freshwater material is therefore often difficult. If the association of elements suggested above for *Palaeolabrus* is correct, then it is an interesting and significant fish, showing some striking advances toward the teleosts in vertebral and premaxillary structure. I do not imply, however, that the *Palaeolabrus* material indicates relationship of primitive teleosts

and amioids. While the general resemblances of *Palaeolabrus* seem to be amioid, there are too many differences from the Amiidae, from other known amioid families, and from known teleosts, to place it in any known family. *Palaeolabrus* should therefore be placed in its own family, Palaeolabridae, n. fam., for which the definition is the same as for the genus. Based on the amioid resemblances of the elements that are clearly referable to *Palaeolabrus,* I include it tentatively in the Order Amiiformes. This questionable reference is difficult to maintain if the elopid-like premaxilla and the teleost-like vertebrae are properly referred (as I believe that they are), but inclusion in any known teleost group on the basis of the known material is much less defensible.

ORDER ELOPIFORMES

SUBORDER ALBULOIDEI

Family Albulidae

Coriops amnicolus, n. gen., n. sp.

Type. American Museum of Natural History (AM) 9317, parasphenoid with attached tooth plate; collected by M. C. McKenna and party, 1960.

Paratypes. AM 9319, four basibranchials and five parasphenoids with attached tooth plates; AM 9301, anterior end of parasphenoid, showing anterodorsal process; AM 9320, pterygoid fragment; other University of California Museum of Paleontology (UC) specimens cited by Estes (1964:49).

Type locality. UC loc. V5620, Lance Formation, Lance Creek, Niobrara County, Wyoming (Clemens, 1963).

Etymology. Greek, *korios,* bug (from the fact that specimens of this fish occur at Bug Creek Anthills); *iops,* a small fish; Latin, *amnicolus,* a river dweller.

Referred specimens. MCZ 9340, five broken parasphenoids with attached tooth plates, Hell Creek Formation, Bug Creek Anthills, west half of section 9, T 22 N, R 17 W, McCone County, Montana, collected by A. D. Lewis and party, 1964. AM 9318, basibranchial with attached tooth plate, and AM 9316, ?pterygoid tooth plate fragment, Lance Formation, UC loc. V5711, Niobrara County, Wyoming, collected by M. C. McKenna and party, 1960.

Diagnosis. An albulid with teeth fused to their attachment areas, basibranchial with well-defined branchial arch attachment areas; parasphenoid with very small otic articulation areas; parasphenoid tooth plates with anteroposterior channel rather than arched as in *Albula.*

Description. Parasphenoid bone compact (Pl. 4a), not arched anteroposteriorly; bone surface coarsely vascularized dorsally; a prominent anterodorsal process present, broken on all specimens in varying degree except in AM 9301; strong "parethmoid" articulation areas present anterolaterally; strong interorbital septum articulation area present on midline; posterolateral surfaces of bone prominently concave; posteriorly, paired slots present posterolaterally for (probably) prootic, apparently no articulation area for basioccipital; teeth styliform, bluntly-pointed, without enameloid tips; tooth-bearing surface of parasphenoid anteroposteriorly-channelled, concave. Basibranchial tooth plate with teeth similar to those of parasphenoid (Pl. 3c), bone convex from side-to-side with essentially straight occlusal border; basibranchial tooth plate teardrop-shaped in small specimens, with the point at the anterior end, larger specimens becoming more symmetrically oval; ventrally, hyoid arch attachment areas well separated; anteriorly a channel present, probably for basihyal plate, followed by paired anteroposterior ridges that probably clasped the basihyal; more posteriorly, an expanded, shallow channel present, probably for basibranchial I; posterior to this a smooth, expanded, and flattened area occurs that probably covered more posterior basibranchial elements (Pl. 4b).

Discussion. No name was originally proposed by Estes (1964) for this fish because of difficulty in comparing specimens of isolated tooth plates and scales, with entire fishes. More recent study (Estes, 1969) has shown that most records of fossil albuloid fishes are based on tooth plates, and that criteria exist for distinguishing the various types regardless of lack of association with whole fishes. The plates described here can be distinguished easily from other albuloid dental plates by the articulation pattern of braincase or palate bones, or hyoid attachment scars, and by the presence of fused teeth.

The bone articulation patterns on parasphenoid and basibranchial are similar to those of *Albula,* especially in the case of the parasphenoid. The major difference from *Albula* is the absence of extensive otic or basioccipital articulation areas (cf. Estes, 1969, figs. 5, 6g); probably these bones (in part) clasped the sides of the parasphenoid, which is more excavated in this region than in that of *Albula.* While the basibranchial scars are identifiable with fair certainty, there are small differences from those of *Albula* and the phyllodontids (Estes, 1969, fig. 2, cf. Pl. 4b, this paper).

The pattern of articulation surfaces on both parasphenoid and basibranchial bones suggests reference to the Albulidae. The existence of only two very closely related genera of living albulids makes it difficult to say whether or not the differences signify more than generic separation from the Recent forms, but I believe that the evident similarities justify allocation to the Albulidae at present.

Little tooth replacement is evident in the dentition of *Coriops;* this feature and its fused teeth separate it clearly from the related phyllodontids. Although many specimens of *Coriops* are present in the Lance Formation sample, only two fragments of pterygoid tooth plates have been identified. They show torsion of the tooth plate as in *Albula,* but no other distinctive features are visible. The presence of pterygoids separates *Coriops* from the phyllodontids, and supports allocation to the albulids.

ACKNOWLEDGEMENTS

I am grateful to Colin Patterson, David Bardack, and Gareth Nelson for helpful comments on the possible relationships of *Palaeolabrus.* Mr. Fred Maynard prepared the photographs. This research was supported in part by NSF grant GB-7176.

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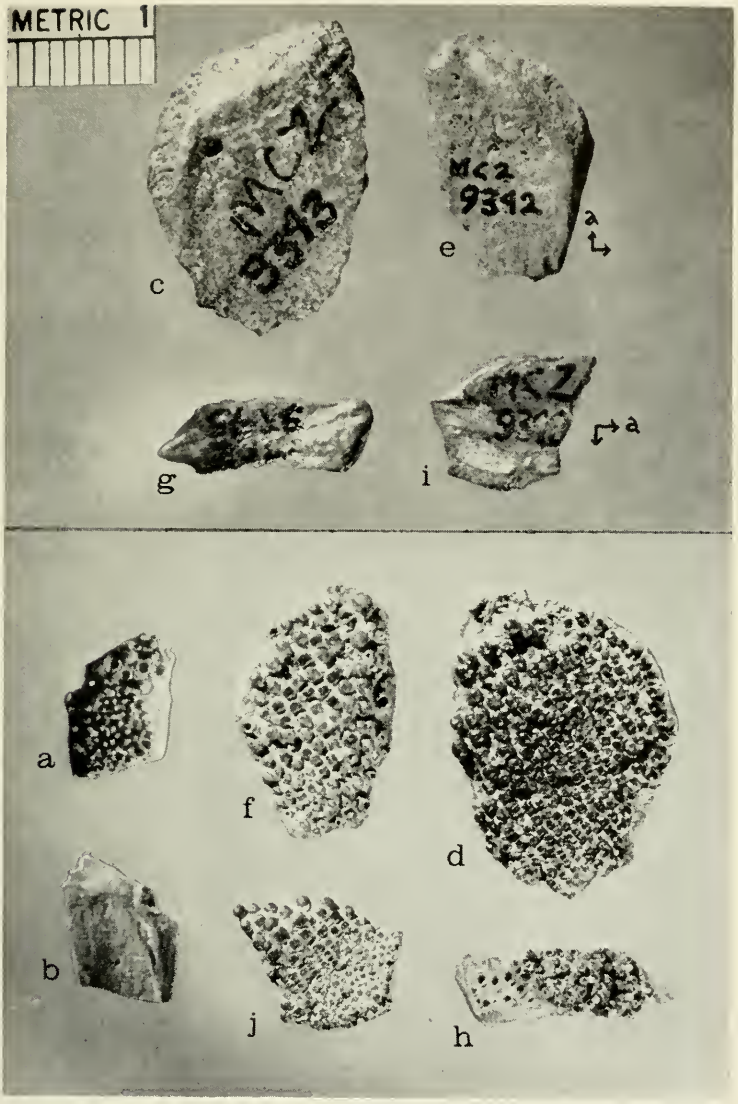

PLATE 1

a — *b*, *Palaeolabrus dormaalensis* Casier, 1967, right vomer (?), Paleogene, Belgium, an Institut Royal de Sciences Naturelles de Belgique specimen not figured in original description, specimen broken posteriorly. *c* — *j*, *P. montanensis*, n. sp., late Cretaceous, Hell Creek Formation, Montana. c — *d*, dorsal and ventral views of type left vomer (?), MCZ 9343; *e* — *f*, the same, paratype right vomer (?), MCZ 9342; *g* — *h*, lateral and medial views of right symphysial coronoid, MCZ 9345; *i* — *j*, dorsal and ventral views of right posterior dermopalatine, MCZ 9380. Arrows = assumed anterior (a) and lateral directions; all × 2.

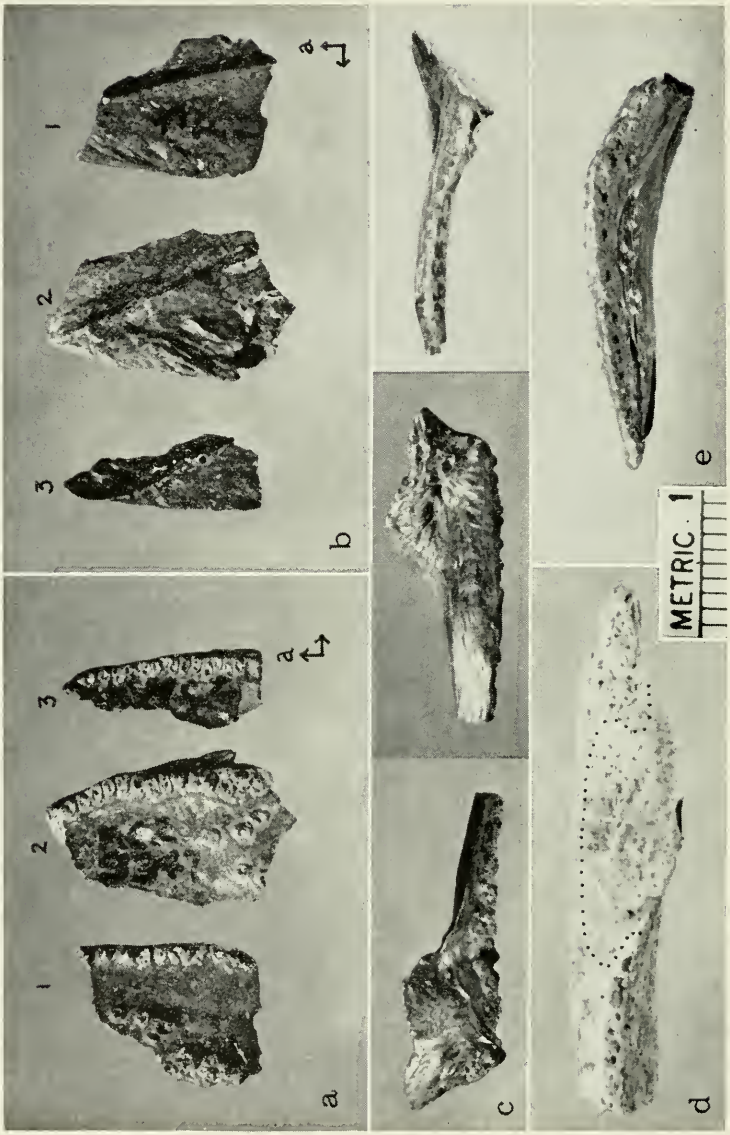
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PLATE 2

Palaeolabrus montanensis, n. sp., late Cretaceous, Hell Creek Formation, Montana. *a,* ventral, and *b,* dorsal views of 1, posterior, 2, intermediate, and 3, anterior fragments of left entopterygoid (?), MCZ 9347; *c,* medial, lateral, and ventral views of referred right premaxilla, MCZ 9346; *d,* occlusal view of posterior end of referred right dentary, MCZ 9341, dotted area outlines fossa for maxilla attachment, *cf.* Pl. 3*a,b; e,* occusal view of anterior end of right dentary, MCZ 9344. Arrows = assumed anterior (a) and lateral views; all × 2.

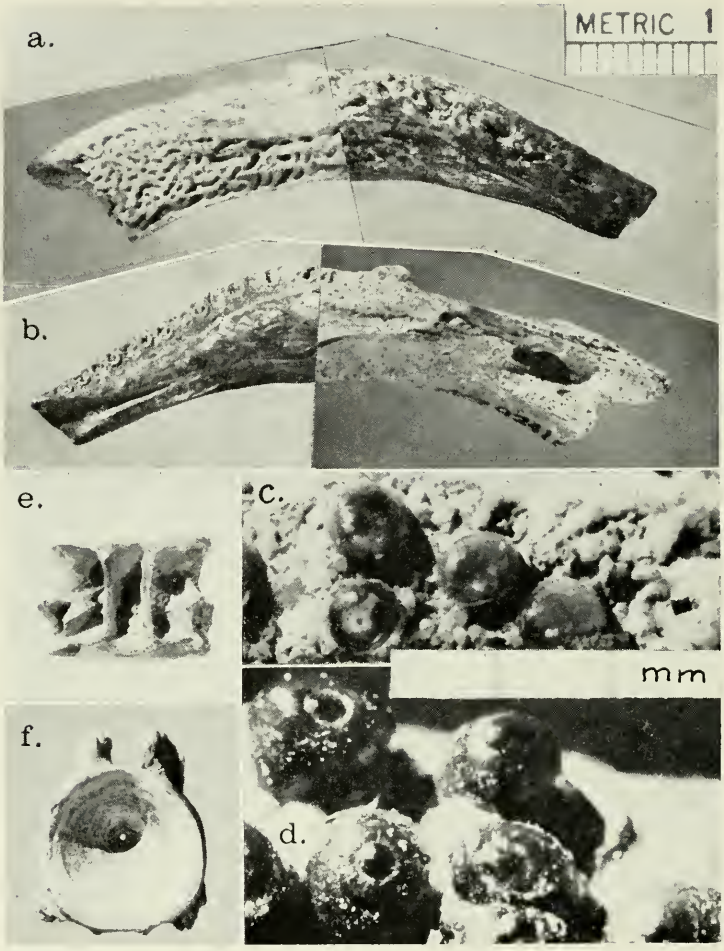

PLATE 3

a, b, d, Palaeolabrus montanensis, n. sp., late Cretaceous, Hell Creek Formation, Montana. *a,* ventral and *b,* dorsal views of composite complete right dentary, anterior end = MCZ 9344, posterior end = MCZ 9341; *d,* much enlarged view of unworn teeth from type left vomer (?), MCZ 9343. *c, Coriops amnicolus,* n. gen., n. sp., late Cretaceous, Lance Formation, Wyoming. Much enlarged view of unworn teeth from basibranchial tooth plate, AM 9319. In *a* — *b,* specimen of posterior end of dentary reduced slightly to fit anterior end, the latter × 2, *c* — *d,* × 15, e — f × 2.

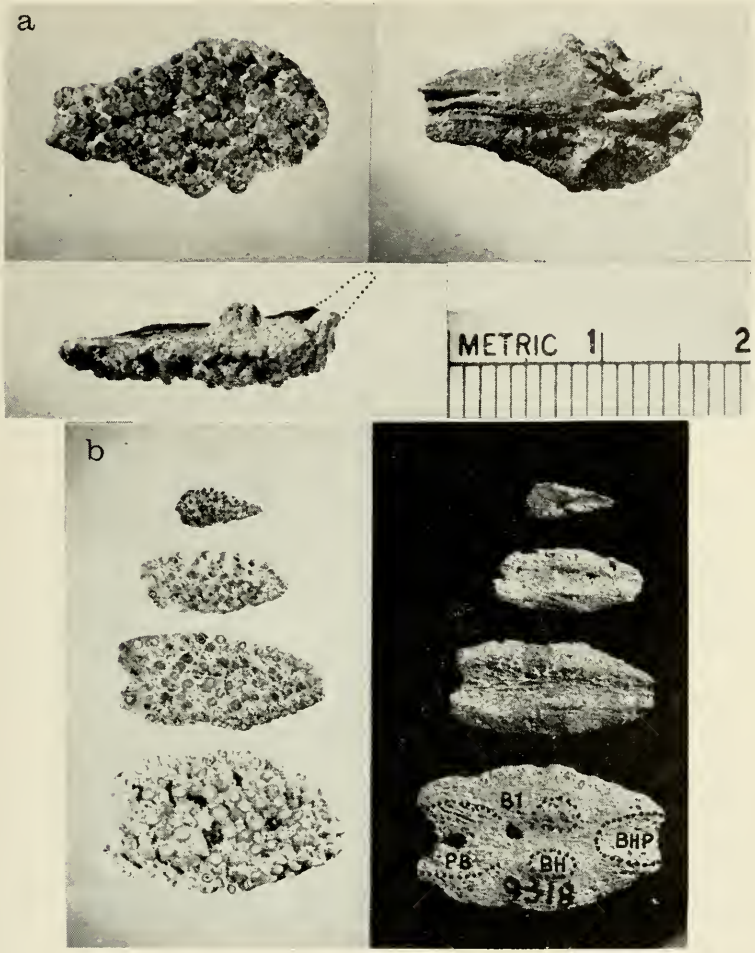

PLATE 4

Coriops amnicolus, n. gen., n. sp., late Cretaceous, Lance Formation, Wyoming. *a,* ventral (occlusal), dorsal, and right lateral views of type parasphenoid tooth plate, AM 9317, anterodorsal process restored in lateral view from AM 9301, locality V5620. *b* (left), dorsal and (right), ventral views of four basibranchial tooth plates to show proportional changes with increasing size, top three specimens = AM 9319, V5620, bottom specimen = AM 9318, V5711; all × 2. Dotted lines = interpreted branchial arch attachment areas, BHP = basihyal plate, BH = basihyal, B1 = first basibranchial, PB = posterior basibranchial elements. Posterior end of bottom three specimens broken, anterior to the right.

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THE STATUS OF THE EAST AFRICAN ELEPHANT "*ARCHIDISKODON EXOPTATUS*" DIETRICH 1942

Vincent J. Maglio

ABSTRACT. The syntype collection of "*Archidiskodon exoptatus*" Dietrich 1942 from Laetolil, east Africa, is reexamined in the light of more recent material from other African localities. The collection is found to be composed of two distinct taxa — one referable to *Elephas recki* Dietrich 1916 and the other to a primitive species of *Loxodonta*. In the interest of nomenclatorial stability, an *E. recki* specimen is chosen as the lectotype of "*A. exoptatus*," thus reducing that name to the junior synonymy of *E. recki*. It is concluded that two faunal horizons are represented in the Laetolil area as suggested by earlier workers, one correlating with both Kanapoi and Yellow Sands at the base of the Omo sequence, and the other correlating with the later Omo beds, possibly antedating Bed I Olduvai by a short time interval.

INTRODUCTION

Since its description by Dietrich in 1942, the name "*Archidiskodon exoptatus*" has been applied to several different taxa by different workers. As a result, the original concept of the species is often misunderstood. Recent concepts have varied from a rather primitive, low-crowned form conspecific with the Upper Siwalik *A. planifrons* (Arambourg, 1947) to a considerably more progressive, higher-crowned form either ancestral to *E. recki* (Cooke, 1960) or synonymous with it as an early stage (Leakey, 1965). Because of the growing significance of the Elephantidae for purposes of correlation, especially in the Plio-Pleistocene of Africa, it is important to establish firmly the status of this taxon in order to avoid further confusion.

The syntype collection of "*Archidiskodon exoptatus*" was collected by Kohl-Larsen during his 1938-1939 expedition to the southern Serengeti in what was then Tanganyika Territory. The fossil localities cover an extensive area south of Olduvai Gorge in the Vogel River area of the Serengeti Plain, just north of Lake

Eyasi. The fossil-bearing Laetolil beds are exposed in the drainage valleys of five river systems — Vogelfluss, Gadjingero, Deturi, Oldogom, and Marambu. The yellow-grey Laetolil tuffs are locally interrupted by a basalt (Kent, 1941), which may represent a fair interval of time. Based on Hopwood's (1936) analysis of the Laetolil fauna, Kent suggested two distinct faunal horizons — one more or less contemporary with Beds I-II at Olduvai, and the other somewhat earlier in the Lower Pleistocene.

Many of the fossils are yellowish white in color and chalky in preservation. Other specimens are brown to black in color and are more highly mineralized. Dietrich considered this difference in preservation, along with morphological differences, as evidence indicating two faunal zones — the "old fauna" and "younger fauna" — thus supporting Kent's earlier view. The yellowish white specimens are the older, the black the younger. He considered the older fossils as products of redeposition, being mixed with material of a considerably later age. Despite this, however, Dietrich believed the entire collection of Proboscidea to be uniform and to represent a single, variable species. Whereas Hopwood (1936) and Kent (1941) recognized two elephantid species in this material — *Palaeoloxodon recki* and *Elephas* aff. *planifrons* — Dietrich considered the Laetolil collection to be a single new species related to the "*E. planifrons-E. meridionalis*" group, but representing a distinct African branch. As I will show below, this view of a single species derived from *E. planifrons* cannot be supported on present evidence. Hopwood's original analysis was essentially correct.

The syntype collection on which Dietrich founded his species consists of 108 molar fragments, nearly all of which are fragmentary or severely worn. Most of these are too incomplete for meaningful diagnosis. Among the 108 specimens the following were identified by Dietrich: $12M^1$, $9M_1$, $5M^2$, $12M_2$, $4M^3$, $24M_3$. The remainder of the collection consisted of milk molars. A reexamination of this collection in the light of the now abundant comparative material from other east African localities shows that a large number of these determinations were incorrect. The mixing of two distinct taxa as well as the misidentification of individual specimens as to their serial position in the tooth row resulted in a specific diagnosis which had little objective relationship to any real taxon. The reasons for this confusion lie not in Dietrich's analysis of the collection, which generally was excellent, but primarily in the fragmentary nature of the material and the lack of

adequate comparative collections at the time he wrote.

The type collection, housed in the Institute for Paleontology, Humboldt University, and six specimens in the British Museum (Natural History) collected several years earlier by Dr. L.S.B. Leakey, have been examined. The material conclusively shows the presence of two taxa, which may be distinguished on morphological grounds and which differ in preservation. These two forms

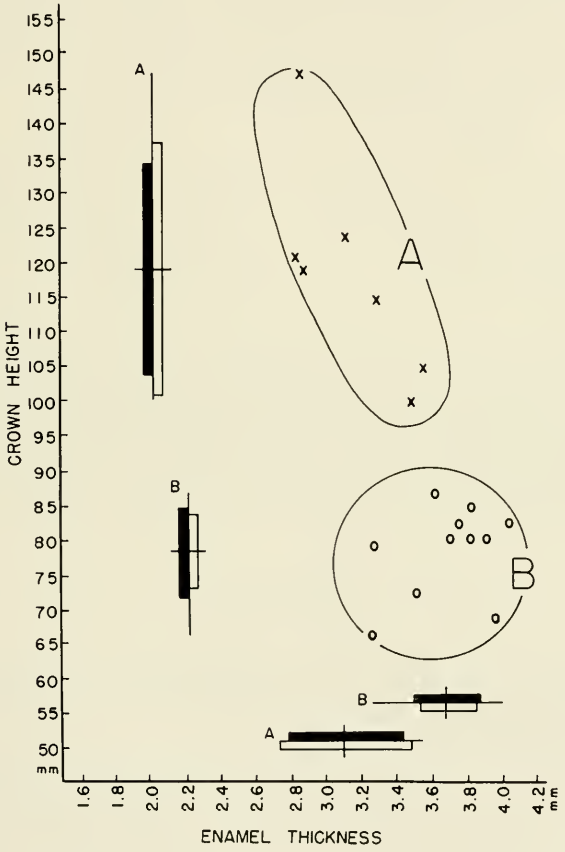

Figure 1. Distribution of first, second, and third permanent molars in the syntype collection of "*Archidiskodon exoptatus*" with respect to enamel thickness and crown height. Group A and B as discussed in text. For each: thin line, observed range; short crossbar, mean; solid rectangle, ± one standard deviation from the mean; open rectangle, 98% confidence interval of the mean.

support the contention that two faunal horizons are present. These can be tentatively correlated with other east African deposits for which acceptable radiometric age determinations are now available (Maglio, in press, a).

The following analysis is based on 37 of the better specimens in the Kohl-Larsen collection and the six British Museum specimens. In Fig. 1 the first, second, and third permanent molars are plotted on a scatter diagram, with average enamel thickness as the abscissa and maximum crown height as the ordinate. Two groups, A and B, separate out on both morphological and metrical criteria. These two groups may be distinguished as follows:

Group A	Group B
Enamel thin and folded	Enamel thicker and smooth
Height/width index for permanent molars 120-200	Height/width index for permanent molars 85-110
11-13 plates on M3	9-11 plates on M3
Weak to absent anterior sinus	Prominent anterior sinus

Similar criteria were used to separate the milk molars. In Tables 1 and 2 the specimens in each group are listed and comparative measurements given. Group A is inseparable on all criteria from *Elephas recki* Dietrich 1916, and group B is very close to a new primitive species of *Loxodonta* from east Africa (Maglio, in press, b).

GROUP A

(Plates I-III)

A total of 19 specimens is included in this group. Unless otherwise stated, all specimens are in the Institute for Paleontology, Humboldt University of Berlin.

M^3. (Pl. III, 7). Two fragmentary specimens of the right side from Vogelfluss. The fragments are too incomplete to allow determination of the total number of plates. It is typical of all the specimens in this group, as it is also for the earlier stages of *E. recki*, that the enamel is only very weakly folded near the apex of the crown but is much more strongly folded toward the base. One specimen (Vo. 11-13/1.39) is in an early stage of wear; the worn plates show rather large, complexly folded posterior loops with smooth to weakly folded enamel on the remainder of the enamel

figure. The lamellar frequency[1] is rather low (3.8), but this fragment is the anterior portion of an M^3; this value is probably lower than the average value for the entire molar. The second specimen (Vo. 330 K.L. 18 9–10. 38) is broken across the basal portion of the crown, revealing a low cross-section of the plates. The median folds are reduced to a slight central widening of the plates, indicating fusion of the anterior and posterior columns into the plate faces. The enamel is strongly folded around the entire surface of the plate. Based on these two incomplete specimens, M^3 may be characterized as follows:

P (no. of plates)=?; L (maximum length)=?; W (width)= 77-94 mm; H (height)=119-121 mm; H/W (100 × height/ width index)= 128-155; LF (lamellar frequency)= 3.8-4.3; ET (enamel thickness)= 2.3-3.4 mm.

M_3. (Pl. I, 1-2; Pl. II, 4-6). Six incomplete molars from Vogelfluss and Gadjingero. The most complete specimens are Z. 94.96 and K.L.-10-13.39, both of the right side. The former bears the last nine plates with the posterior root system underlying the last eight. From the position of the posterior and intermediate root bases, this molar must have had at least three and more likely four additional anterior plates, making a total of 12-13. As in M^3, the enamel is little folded near the apex but is much more so toward the base. Thus, no. Z. 94.96, which has only the first five preserved plates in wear, has nearly smooth enamel except on the first and most worn plate, which is just beginning to show weak folding in the median portion of the enamel figure. G.K.-18 is a well worn specimen with columns that are nearly completely fused into the plate faces. The enamel is coarsely folded, especially in the median portion of the enamel figures. Anterior columns are generally small or lacking entirely, whereas the posterior ones are free at the apex. The latter form prominent loops or sinuses on the enamel figures of moderately worn plates, but these disappear in later stages of wear as the columns become fused into the plates toward the base. M_3 may be characterized as follows:

P=12-13; L=approx. 250-300 mm; W=70-88 mm; H=100-147 mm; H/W=122-198; LF=4.3-5.4; ET=2.6-3.9 mm.

[1] The average number of plates in a distance of 10 cm measured parallel to the crown base.

M^2. One incomplete left molar from Garussi, a tributary of Vogelfluss (no number). Although lacking its lingual half, this specimen is complete as to length and has nine plates plus a strong posterior heel. The enamel is moderately folded and there is a small but prominent posterior sinus. It is too worn for determination of the crown height.

P=9; L=176 mm; W=?; H=?; H/W=?; LF=6.0; ET=3.1-3.8 mm.

M_2. A single specimen (G.K. 1/39) from Garussi. Only the anterior three plates are preserved. From what remains, this molar appears to have been similar to M^2.

P=?; L=?; W=77 mm; H=?; H/W=?; LF=5.2; ET=2.4-2.8 mm.

M^1. One incomplete specimen (Vo. Aa) with the first five plates preserved. The crown is too worn for a determination of its height.

P=?; L=?; W=62.1 mm; H=?; H/W=?; LF=5.3; ET=2.7-2.9 mm.

M_1. (Pl. I, 3). One partial specimen (Vo. A) from Vogelfluss. The last five plates and a strong posterior heel are preserved. The wear figures form a narrow loxodont pattern, without strong median sinuses but with angular median expansions. The enamel is strongly folded. The specimen is too worn for a determination of the crown height.

P=?; L=?; W=66 mm; H=?; H/W=?; LF=5.1; ET=2.1-3.0 mm.

dM^4. One incomplete specimen (BM L. 171 QS). Six plates are preserved and it is probable that this represents the total number for this tooth. The crown is short and broad with thin, coarsely folded enamel and only slight median expansions; there are no true sinuses.

P=6; L=106 mm; W=82 mm; H=?; H/W=?; LF=5.7; ET=1.6-2.2 mm.

dM_4. Two incomplete teeth (G.K. 2/39 and Vo. 313 2b(7.73)) from Vogelfluss and Garussi. These specimens are too fragmentary to allow a determination of the crown height or the number of plates. From what remains, we may characterize this molar type as follows:

P=?; L=?; W=56-59 mm; H=?; H/W=?; LF=5.9-7.3; ET=1.7-2.4 mm.

dM_3. (Pl. III, 8-9). One complete specimen (BM M-14942) from Vogelfluss. There are six plates and a very strong heel. The apices of the plates are divided into numerous small digitations

with remnants of a slightly deeper median cleft showing in very early stages of wear. Weak median sinuses are seen on moderately worn plates and the enamel is thin and strongly folded. A strong anterior root supports the first two plates; a small internal intermediate root supports portions of both the third and fourth plates, and the posterior root supports plates 4-6 and the heel.

P=6; L=73.5 mm; W=37 mm; H=31 mm; H/W=85; LF=8.1; ET=1.3-1.7 mm.

dM^2. (Pl. III, 10-11). Two complete specimens (Z.60 and Z.68) from Vogelfluss and Garussi. Z.68 is unworn and bears three plates as well as a strong two-cusped anterior ridge. A posterior heel consists of seven small columns closely appressed to the last true plate. The tooth is narrow anteriorly but broadens considerably at the second plate and is widest at the third. A stout root supports the last two plates and the heel; a second root supports the anterior ridge and first true plate.

P=3; L=25-27 mm; W=22 mm; H=13-18 mm; H/W=58-80; ET=1.1 mm.

dM_2. (Pl. III, 12-13). One complete specimen (Z.62) from Garussi. There are four plates plus a strong posterior heel. As in dM^2, the tooth broadens posteriorly but not nearly as much. The first two plates have only three digitations, the third has five, and the fourth, eight. Two roots are present as in dM^2.

P=4; L=26.5 mm; W=18 mm; H=14 mm; H/W=77; ET=?.

This assemblage of molars as a whole compares well with material from other east African localities, such as Olduvai Beds I-II, and the upper part of the Omo sequence, which are referable to different stages of *Elephas recki*. As discussed elsewhere (Maglio, in press, a, and Cooke and Coryndon, in press), the most primitive stage (stage 1 of Maglio) attributable to *E. recki* occurs at Kikagati, Uganda (Hopwood, 1939), a deposit which appears to be equivalent to the upper Kaiso beds (H.B.S. Cooke, pers. comm.). This form, originally referred to *"Archidiskodon griqua"* by Hopwood, has approximately 13 plates on the M_3, a lamellar frequency of 4-5, and a height/width index of about 120-135. The enamel is relatively thick (2.8-3.3 mm) and smooth, lacking the characteristic folding of later stages of this species. Large anterior and posterior sinuses are formed with wear due to the presence of median columns fused for the most part to the surfaces of the plates. The posterior columns may be free at their apices, and are generally lower in height than the associated plates. As a result, the sinuses do not appear in the enamel figure until intermediate stages of wear.

Successively more progressive stages of *E. recki* are found in the later Omo beds, Beds I-II Olduvai, and in Bed IV Olduvai. The later Omo stage (stage 2 of Maglio, *op. cit.*) has, on the average, slightly thicker enamel than does the Laetolil material, and is proportionately slightly lower crowned. The lamellar frequency is greater (5-6) and the number of plates appears to have been slightly higher. The worn enamel figures show little or no development of an anterior sinus, but a persistent fused posterior column is present as in the Laetolil material. The enamel is only weakly folded in the median portion of the plates.

The Olduvai Bed I-II form (stage 3) is somewhat more progressive than the Omo and Laetolil form, having generally thinner, more highly folded enamel and reduced, irregular sinuses.

The Laetolil assemblage as a whole would apear to be closest to the later Omo population of *Elephas recki*. Based on the elephants, at least part of the Laetolil fossiliferous beds may be correlated with this part of the east African sequence.

GROUP B

(Plates IV-VI)

Twenty-four specimens are included here as follows:

M^3. (Pl. IV, 14-15). Three incomplete specimens (BM M-15416, G.K. V, and Vo. 70) from Vogelfluss and Garussi. The most complete specimen (BM M-15416) bears the last seven plates and probably had no more than nine or ten when complete. Only the last plate permits a measure of the crown height (68.0 mm), but the maximum height must have been 15-20 mm greater. The enamel is thick and not folded. Anterior and posterior sinuses are present on the plates in intermediate stages of wear. The plates are well spaced — there are only 3.5 in 10 cm. G.K. V is unworn but has been sectioned at about the middle of its height. Except for slight coarse folding of the enamel in the median part of the wear figure, the enamel is smooth as in the previous specimen.

P=?9-10; L=?; W=76-85 mm; H=68-83 mm; H/W=96-109; LF=3.5-4.3; ET=3.3-4.3 mm.

M_3. Two incomplete specimens (BM LS 9VI35 and Vo. 9-10.3B). The height/width index of the one unworn specimen (BM LS 9VI35) is very low, and it is likely that the average height for this molar type was somewhat greater. Other characters are as in M^3.

P=?; L=?; W=87-94 mm; H=79 mm; H/W=85; LF=3.4-4.0; ET=3.0-3.7 mm.

M^2. One specimen (G.K. 2.39II) from Garussi. The last six plates are preserved and the last three are unworn. The enamel is thick and unfolded.

P=?; L=?; W=80 mm; H=72 mm; H/W=91; LF=4.9; ET=3.4-3.6 mm.

M_2. (Pl. IV, 16; Pl. V, 18-21). Five incomplete specimens from Vogelfluss and Garussi. The most complete specimen (Vo. 9/10.38) bears the last seven plates with the posterior root system supporting the last five. A strong anterior root underlies the first one and one-half plates suggesting that the tooth is essentially complete except for a probable anterior ridge and perhaps one additional plate. The plates are thin toward their apices but broaden rapidly toward the base. The wear figures are widest in the midline and have rounded anterior and posterior sinuses. The enamel is thick and not folded. In another specimen (Vo. N), the sinuses are larger and the enamel is somewhat wavy, although not folded as in *E. recki*. The posterior columns may be free for part of their height, as in no. 5882, becoming fused with the plate face toward the base. The transverse valleys between the plates are broadly open and U-shaped. As in other molars in this group, the crown height is roughly equivalent to its width. This molar type is characterized as follows:

P=7-8; L=approx. 200 mm; W=81-88 mm; H=80-87 mm; H/W=91-106; LF=4.2-5.0; ET=3.1-4.5 mm.

M_1. (Pl. VI, 22-23). Five specimens from Vogelfluss and Garussi. Two specimens (5828 and 5824) are complete but well worn, and probably represent the left and right tooth of the same individual. Both have the anterior plates worn down to the root, but from the position of the anterior root, it is clear that the total number of plates was seven. The last plate is only slightly worn and offers a means of estimating the maximum crown height (about 80 mm). The enamel is thick and smooth. Prominent sinuses are present on several of the worn plates. The enamel figure indicates the presence of a weak median cleft on the upper half of the anterior four or five plates. A strongly backward-curving anterior root supports the first one and one-half plates; an equally strong and curved intermediate root underlies the lingual half of plates 3 and 4. The posterior root system supports the last three plates.

P=7; L=155-165 mm; W=69-88 mm; H=67-80 mm; H/W=96-99; LF=4.6-5.1; ET=2.5-4.0 mm.

dM_3. (Pl. IV, 17). Two nearly complete specimens (Vo. 330 (7.78) and 5827) from Vogelfluss. Both specimens have five

plates as well as a small posterior heel. Prominent anterior and posterior columns are fused into the plates for their entire height and with wear form sharp sinuses. Though slightly wavy, the enamel is essentially smooth and rather thick.

P=5; L=126 mm; W=51-58 mm; H=?; H/W=?; LF=5.0-5.9; ET=2.0-3.2 mm.

dM^3. Two specimens from Vogelfluss and Garussi. No. 5818 is complete, with five plates, an anterior ridge, and a posterior heel. The enamel is weakly folded around the entire surface of the plates. There are weak median loops on the enamel figure in early stages of wear, but these become more prominent with increased wear. The second specimen (5830) has larger sinuses and a deep median cleft on the first two plates.

P=5; L=71 mm; W=39-41 mm; H=32-42 mm; H/W=78-92; LF=8.1-8.3; ET=1.2-2.0 mm.

dM_3. (Pl. VI, 24-25). Two specimens (5883 and 5886) from Vogelfluss and Garussi. Six plates are preceded by a small anterior ridge. The enamel is weakly but very coarsely folded and the wear figure is very irregular. Small median swellings on the anterior and posterior faces of the plates mark the position of the fused columns. The tooth is proportionately wider than the corresponding tooth of *E. recki* and has one less plate. An anterior root supports the first one and one-half plates, and the posterior root system supports the last four.

P=6; L=54-71 mm; W=35-37 mm; H=31 mm; H/W=84; LF=9.3-9.5; ET=1.5-2.0 mm.

dM_2. (Pl. VI, 26-27). Two complete specimens (5837M and 5837G) from Marambu and Garussi. This is smaller and proportionately less elongated than the corresponding tooth of *E. recki*. There are only three plates present with a small anterior ridge and a posterior heel. The plates have only three to four digitations in contrast to the 7-8 of *E. recki*. Unlike the condition in the latter species, there is only a single root, constricted vertically into an anterior and posterior portion.

P=3; L=19-22 mm; W=15-16 mm; H=14-16 mm; H/W=86-102; ET=1.2 mm.

The twenty-four specimens in the present group B certainly represent a form considerably more primitive than that of group A in every trait that can be used to characterize the evolution of molars in elephants. In Table 3, ranges of measurements are summarized for the six molars of each group. The available measurements and the morphology of specimens in group B are close to

Kanapoi species "C" of Maglio (in press, a) and to those of *Mammuthus africanavus*. The major differences between these latter two species lie in the skull. A poorly preserved skull from north Africa (Arambourg, in press) has been referred to *M. africanavus* and demonstrates the *Mammuthus* affinities of this species. However, a skull and skeleton of Kanapoi species "C" (Maglio, in press, b) demonstrates its ancestral relationship to *Loxodonta africana*. Though very similar in dentition, these two fossil species can be distinguished on teeth alone when a suitable sample is available; there are 1-2 fewer plates in the Kanapoi species, the plates do not taper toward the apex as markedly as in *M. africanavus*, and the median sinuses are generally larger. Molars from lower Kaiso, Yellow Sands (Omo), the Chemeron beds, and Kanam are also referable to Kanapoi species "C." The Laetolil elephant here referred to group B appears also to belong here.

DISCUSSION

As for the status of *"Archidiskodon exoptatus,"* it is clear that the name encompasses two distinct taxa, one (*E. recki* Dietrich 1916) with priority. It is my opinion that the name *"A. exoptatus"* should be suppressed for the following reasons: 1) The concept of the species as originally intended has been confused in the literature to the point where recent workers cannot be certain of the proper diagnosis. Even if adequately limited to one good taxon, the name would still invoke confusion in the minds of some workers who must deal with the past literature. 2) With the availability of the excellent and abundant new material from Kanapoi and other localities, it is unwise to maintain the fragmentary material from Laetolil as the type collection of any species. Though part of this collection is probably conspecific with the Kanapoi species of *Loxodonta*, identity with this taxon (or any other) can not be certain on present evidence. Where possible, fossil species should be founded on the most adequate material available.

Since Dietrich did not select a type specimen, I, as first revisor, select as the lectotype of *"A. exoptatus"* IPUB no. Z. 94-96, a right M_3 of group A. Thus, *Archidiskodon exoptatus* Dietrich 1942 becomes a junior synonym of *Elephas recki* Dietrich 1916. The present group B is then referred to *Loxodonta* sp., pending description of the new species from Kanapoi.

CONCLUSIONS

The occurrence of two species at Laetolil tends to confirm earlier suggestions that the Laetolil fauna represents two distinct horizons. One, containing a stage 2 *E. recki,* correlates best with the later Omo beds, and may antedate Bed I Olduvai, but only by a relatively short interval of time. The second and earlier fauna with a primitive species of *Loxodonta* seems to correlate best with Kanapoi, Yellow Sands, Chemeron, and Kanam. Both species occur at the Vogelfluss and Garussi exposures, but only *E. recki* has been recorded from the Gadjingero exposures. The significance of this is uncertain. The drainage of the Gadjingero lies to the north of both Vogelfluss and Garussi and generally at a higher altitude. It is possible that it includes only the upper levels of the Laetolil beds. Whether several distinct levels are involved as proposed by Kent (1941), or whether we are dealing with redeposition and mixing of two faunas at a single horizon as suggested by Dietrich (1942) is not certain on present evidence.

ACKNOWLEDGEMENTS

I wish to express my gratitude to Dr. Karl-Heintz Fischer of the Institut für Paläontologie u. Museum, the Humboldt University of Berlin for permission to examine and photograph the syntype collection of *"A. exoptatus,"* and to Dr. Anthony Sutcliffe of the Department of Vertebrate Paleontology, British Museum (Natural History) for permission to study relevant specimens in the collections of that institution. I am grateful to Professor Camille Arambourg for allowing me to examine unpublished material in his collection. Thanks are also due to Professor H. B. C. Cooke and Mrs. Shirley Coryndon for allowing me to see their unpublished manuscript on the Kaiso beds and for permission to study specimens discussed in that work. Professors Bryan Patterson and H. B. S. Cooke kindly read the manuscript and offered helpful comments.

The research was supported in part by NSF Grant nos. GP-1188 and GA-425 to Professor B. Patterson and by an Evolutionary Biology Training Grant to the Department of Biology, Harvard University, NSF Grant no. BG-7346 (Reed C. Rollins, principal investigator).

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(Received 19 August 1969.)

ABBREVIATIONS

BM — British Museum (Natural History).
IPUB — Institut für Paläontologie u. Museum, der Humboldt Universität zu Berlin.

TABLE 1

Measurements of the nineteen specimens of "group A" from Laetolil.

Abbreviations: P, no. of plates; L, length; W, width; H, height; H/W, 100 × height/width; LF, lamellar frequency; ET, enamel thickness. Superscripts indicate the number of the plate from the front on which the measurement was taken; superscript "e" indicates an estimated value.

Museum Number		P	L (mm)	W (mm)	H (mm)	H/W	LF	ET (mm)
IPUB Vo. 11-13/1.39	r.M^3	$+\frac{1}{2}2\frac{1}{2}+$	81.2+	94.1^1	120.8^4	128	3.8	2.5-3.1
IPUB Vo. 330 (K.L.18/9-10.38)	r.M^3	+3	79.5+	77.0^2	119.0^2	155	4.3	2.3-3.4
IPUB Z. 94.96	r.M_3	+9	208.8+	86.8^3	115.0^e	140	5.1	3.0-3.5
IPUB G.K.-18	l.M_3	+7	156.4+	85.4^1	—	—	4.6	3.2-3.9
IPUB K.L.-10-13.3.39	r.M_3	+8+	207.5+	88.0^3	147.2^e	172	4.6	2.6-3.0
IPUB Vo. 11/13.1.39	l.M_3	+4+	82.4+	67.9^2	124.0^1	198	4.9	2.7-3.5
IPUB Vo. 11/13.1.39A	l.M_3	+4+	74.6+	70.5^2	100.0^2	142	4.3	3.0-3.9
IPUB G. 2/39	l.M_3	+5+	93.4+	85.7^2	105.3^3	122	5.4	3.5-3.6
IPUB G.K. ?	l.M^2	9+	175.6+	—	—	—	6.0	3.1-3.8
IPUB G.K. 1/39	l.M_2	3+	71.0+	76.7^3	—	—	5.2	2.4-2.8
IPUB Vo. Aa	M^1	5+	93.1+	62.1^3	—	—	5.3	2.7-2.9
IPUB Vo. A	M_1	+5	109.0+	65.9^3	—	—	5.1	2.1-3.0
BM L. 171 QS	l.dM^4	?6	105.9+	82.1^2	—	—	5.7	1.6-2.2
IPUB G.K. 2/39	l.dM_4	+4	81.3+	58.5^3	—	—	5.9	1.7-2.4
IPUB Vo. 313 2b(7.73)	dM_4	+3	46.2+	56.1^2	—	—	7.3	1.9-2.4
BM M-14942	l.dM_3	6	73.5	36.7^5	36.0^6	85	8.1	1.3-1.7
IPUB Z. 68	l.dM^2	3	25.4	21.9^3	17.5^1	80	—	—
IPUB Z. 60	l.dM^2	3	27.2	21.9^2	12.8^e	58	—	1.1
IPUB Z. 62	l.dM_2	4	26.5	18.2^3	14.0^1	77	—	—

TABLE 2

Measurements of the twenty-four specimens of "group B" from Laetolil.
See Table 1 for abbreviations.

Museum Number		P	L (mm)	W (mm)	H (mm)	H/W	LF	ET (mm)
IPUB G. K. V	r.M^3	+½4	125.9+	82.7[1]	80.0[1]	96	4.3	3.3-4.1
BM M-15416	r.M^3	+7+	194.1	85.0[5]	68.0[7]	96[e]	3.5	3.6-4.3
IPUB Vo. 70	r.M^3	+4	105.3+	76.0[2]	82.5[c]	109	4.3	3.8-4.2
BM LS 9VI35	l.M_3	+4+	132.2+	94.4[2]	79.1[2]	85	3.4	3.0-3.5
IPUB Vo. 9-10.3B	l.M_3	3½+	107.2+	86.9[3]	—	—	4.0	3.0-3.7
IPUB G. K. 2.3911	r.M^2	+6	101.0+	79.5[1]	72.1[3]	91	4.9	3.4-3.6
IPUB Vo. 9/10.38	r.M_2	+7	191.1	83.6[4]	—	—	5.0	—
IPUB 5823	l.M_2	+4	91.2+	81.8[2]	87.0[e]	106[e]	4.2	3.3-3.9
IPUB Vo. C	M_2	+2+	—	81.2	85.0	105	4.6	3.1-4.5
IPUB 5882	l.M_2	+5	140.8+	87.8[2]	80.0[e]	91[c]	4.3	3.4-4.4
IPUB Vo. N	r.M_2	+6	178.1+	86.2[3]	82.3[4]	97	4.6	3.4-4.1
IPUB 5828	l.M_1	7	155.0	87.5[5]	—	—	4.8	3.5-3.9
IPUB 5824	r.M_1	7	165.0	82.6[5]	80.0[e]	99[e]	4.6	3.6-4.0
IPUB Vo. 330	M_1	3+2	—	69.3[4]	66.5[5]	96	5.1	2.8-3.7
BM S 12VI35	M_1	+3+	64.1+	—	—	—	4.9	2.5-3.0
BM S 12VI35	M_1	4+	72.1+	—	—	—	4.3	3.3-3.5
IPUB Vo. 330 (7.78)	l.dM_4	5	90.8+	51.5+	—	—	5.9	2.0-3.2
IPUB 5827	r.dM_4	5	126.4	57.8[4]	—	—	5.0	2.5-3.0
IPUB 5818	l.dM^3	5	71.0	41.0[3]	32.0[5]	78[e]	8.3	1.2-2.0
IPUB 5830	l.dM^3	4+	61.0+	39.0[4]	42.5[4]	92	8.1	1.9-2.0
IPUB 5883	l.dM_3	6	71.2	37.0[4]	31.1[5]	84	9.5	1.6-1.8
IPUB 5886	l.dM_3	6	54.0	35.1[3]	—	—	9.3	1.5-2.0
IPUB 5837M	r.dM_2	3	21.5	15.3[3]	15.6[1]	102	—	1.2
IPUB 5837G	l.dM_2	3	19.2	16.0[2]	13.7[2]	86	—	—

TABLE 3

Comparative measurements of *Elephas recki* and *Loxodonta* sp. from Laetolil.

M^3	No. of plates	H/W	LF	ET (mm)	N
Elephas recki	?	128-155	3.8-4.3	2.3-3.4	2
Loxodonta sp.	9-10	96-109	3.5-4.3	3.3-4.3	3
M_3					
Elephas recki	12-13	122-198	4.3-5.4	2.6-3.9	6
Loxodonta sp.	?	84	3.4-4.0	3.0-3.7	2
M^2					
Elephas recki	9	—	6.0	3.1-3.8	1
Loxodonta sp.	?	91	4.9	3.4-3.6	1
M_2					
Elephas recki	—	—	5.2	2.4-2.8	1
Loxodonta sp.	7-8	91-106	4.2-5.0	3.1-4.5	5
M^1					
Elephas recki	—	—	5.3	2.7-2.9	1
Loxodonta sp.	—	—	—	—	0
M_1					
Elephas recki	—	—	5.1	2.1-3.0	1
Loxodonta sp.	7	96-99	4.6-5.1	2.5-4.0	5
dM^4					
Elephas recki	6	—	5.7	1.6-2.2	1
Loxodonta sp.	—	—	—	—	0
dM_4					
Elephas recki	—	—	5.9-7.3	1.7-2.4	2
Loxodonta sp.	5	—	5.0-5.9	2.0-3.2	2
dM^3					
Elephas recki	—	—	—	—	0
Loxodonta sp.	5	78-92	8.1-8.3	1.2-2.0	2
dM_3					
Elephas recki	6	85	8.1	1.3-1.7	1
Loxodonta sp.	6	84	9.3-9.5	1.5-2.0	2
dM^2					
Elephas recki	3	58-80	—	1.1	2
Loxodonta sp.	—	—	—	—	0
dM_2					
Elephas recki	4	77	—	—	1
Loxodonta sp.	3	86-102	—	1.2	2

PLATES

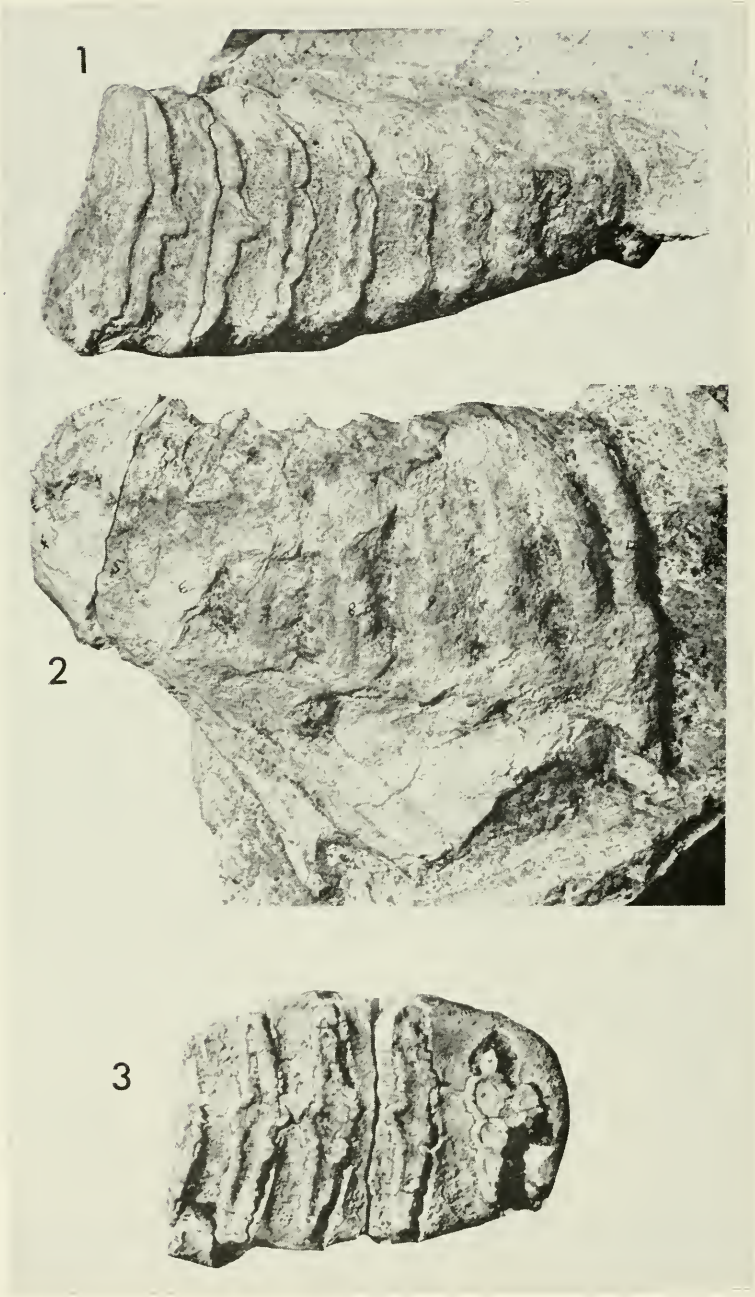

Plate I

1. *Elephas recki*, IPUB Z. 94.96, r.M_3; occlusal view. × 2/5.
2. *Elephas recki*, IPUB Z. 94.96, r.M_3; lingual view. × 2/5.
3. *Elephas recki*, IPUB Vo. A, r.M_1; occlusal view. × 1/2.

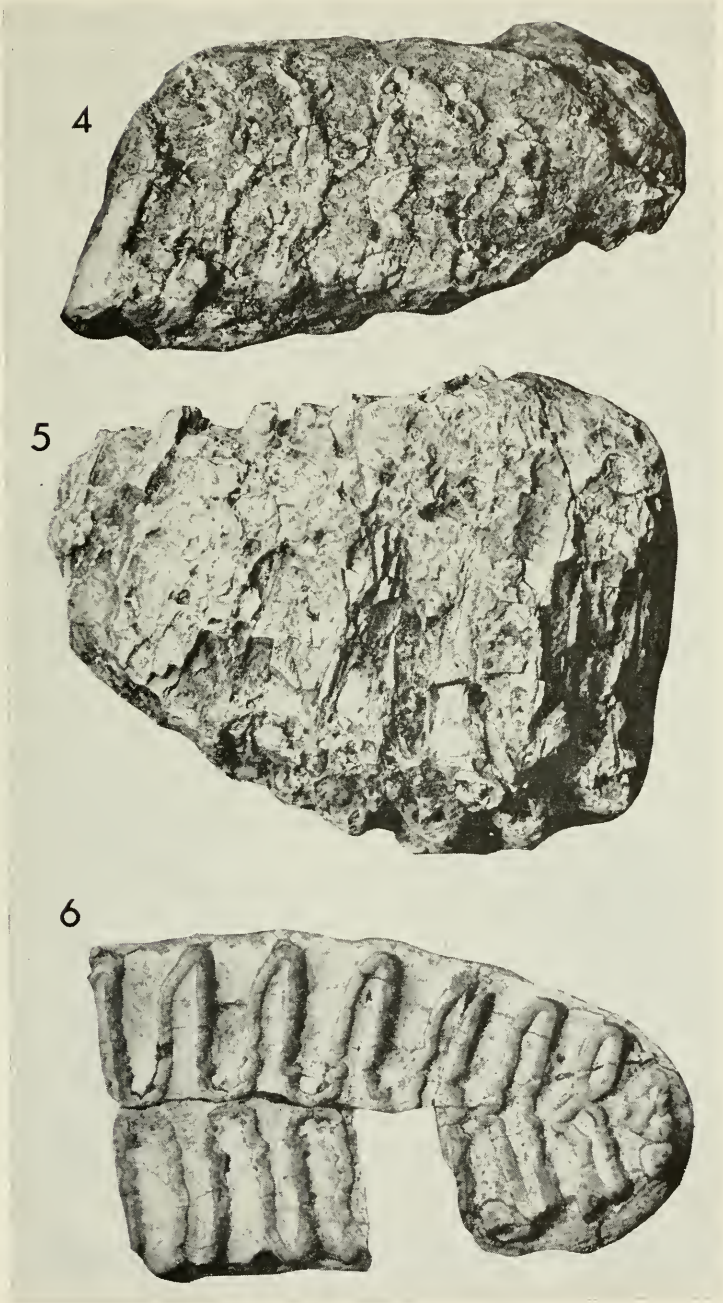

Plate II

4. *Elephas recki*, IPUB K. L. 10-13.3.39, r.M_3; occlusal view. × 2/5.
5. *Elephas recki*, IPUB K. L. 10-13.3.39, r.M_3; lingual view × 2/5.
6. *Elephas recki*, IPUB G. K.-18, l.M_3; occlusal view. × 1/2.

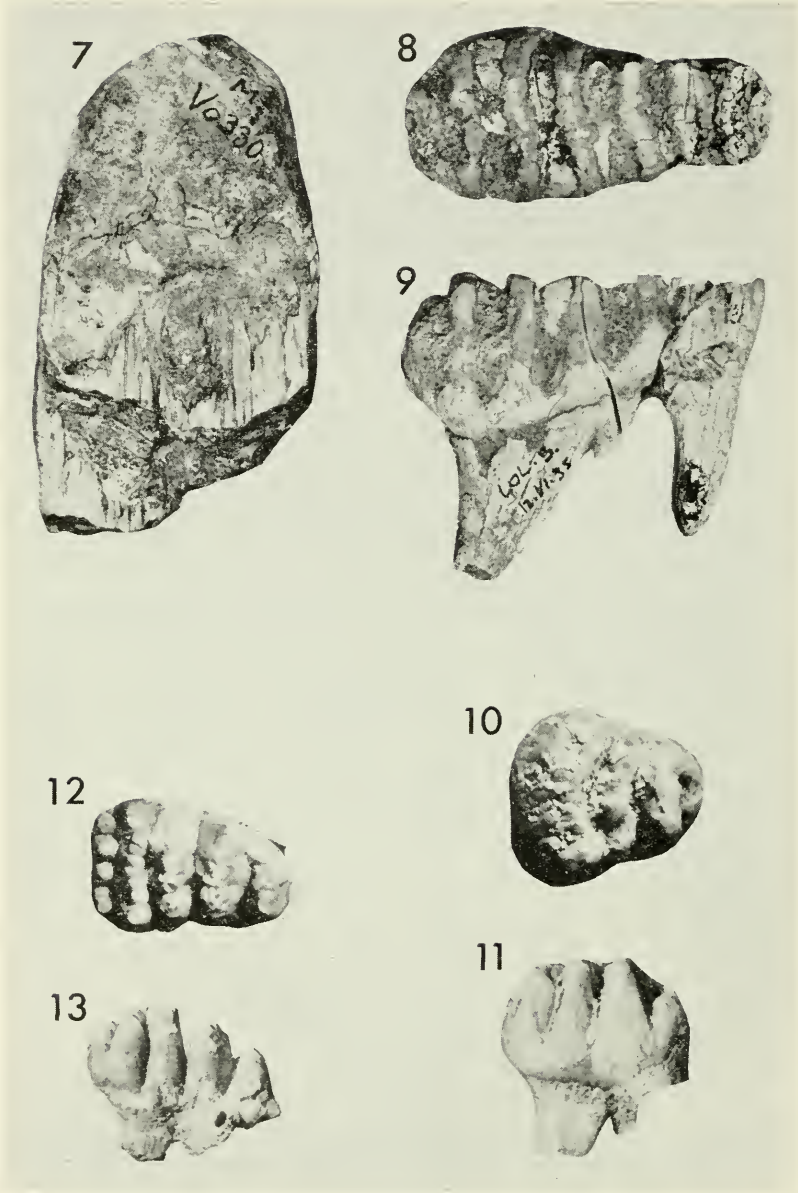

Plate III

7. *Elephas recki,* IPUB 330 (K. L. 18/9-10.38), r.M^3; anterior view. × 1/2.
8. *Elephas recki,* BM M-14942, l.dM_3; occlusal view. × 2/3.
9. *Elephas recki,* BM M-14941, l.dM_3; lingual view. × 2/3.
10. *Elephas recki,* IPUB Vo. Z.68, l.dM^2; occlusal view. × 1.
11. *Elephas recki,* IPUB Vo. Z.68, l.dM^2; lingual view. × 1.
12. *Elephas recki,* IPUB Z. 62, r.dM_2; occlusal view. × 1.
13. *Elephas recki,* IPUB Z. 62, r.dM_2; buccal view. × 1.

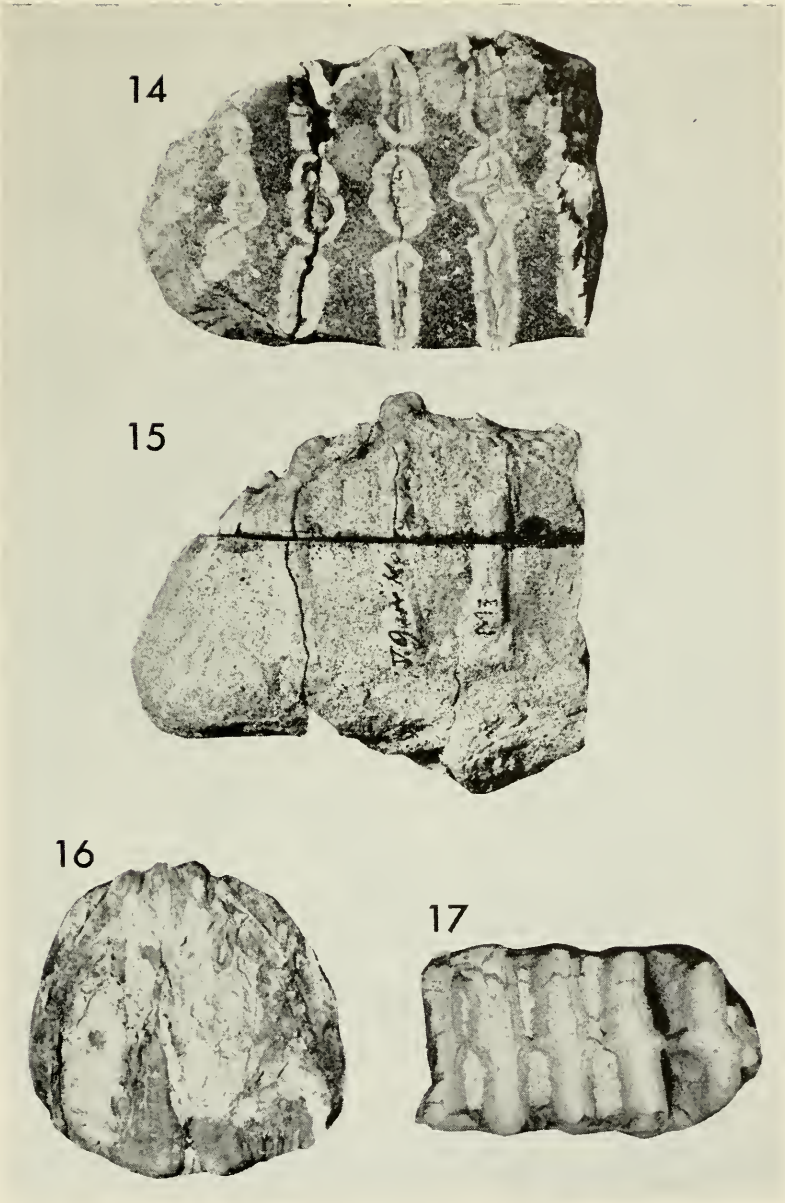

Plate IV

14. *Loxodonta* sp., IPUB G.K. V, r.M^3; sectioned surface. × 1/2.
15. *Loxodonta* sp., IPUB G.K. V, r.M^3; lingual view. × 1/2.
16. *Loxodonta* sp., IPUB Vo. C, M_2. × 1/2.
17. *Loxodonta* sp., IPUB Vo. 330 (7.78), r.dM_4; occlusal view. × 1/2.

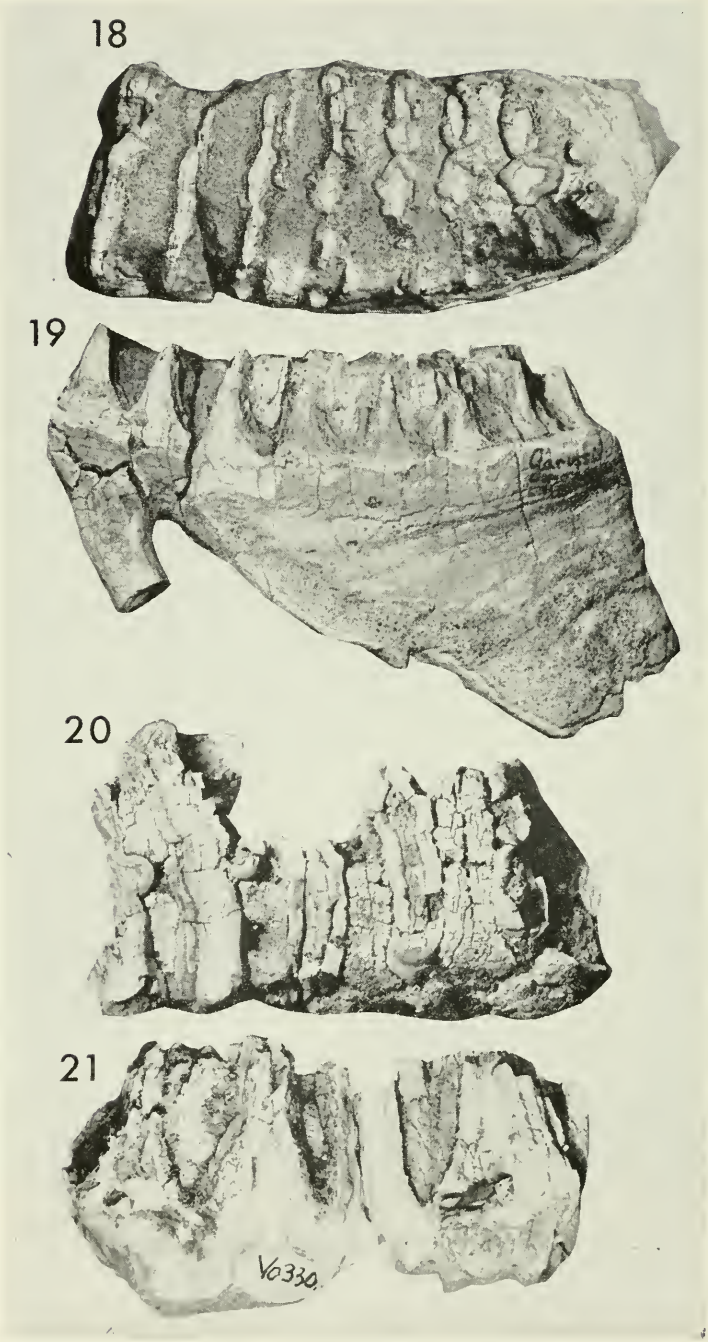
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Plate V.

18. *Loxodonta* sp., IPUB 9/10-38, r.M_2; occlusal view. × 2/5.
19. *Loxodonta* sp., IPUB 9/10-38; r.M_2; lingual view. × 2/5.
20. *Loxodonta* sp., IPUB 5882, l.M_2; occlusal view. × 1/2.
21. *Loxodonta* sp., IPUB 5882, l.M_2; lingual view. × 1/2.

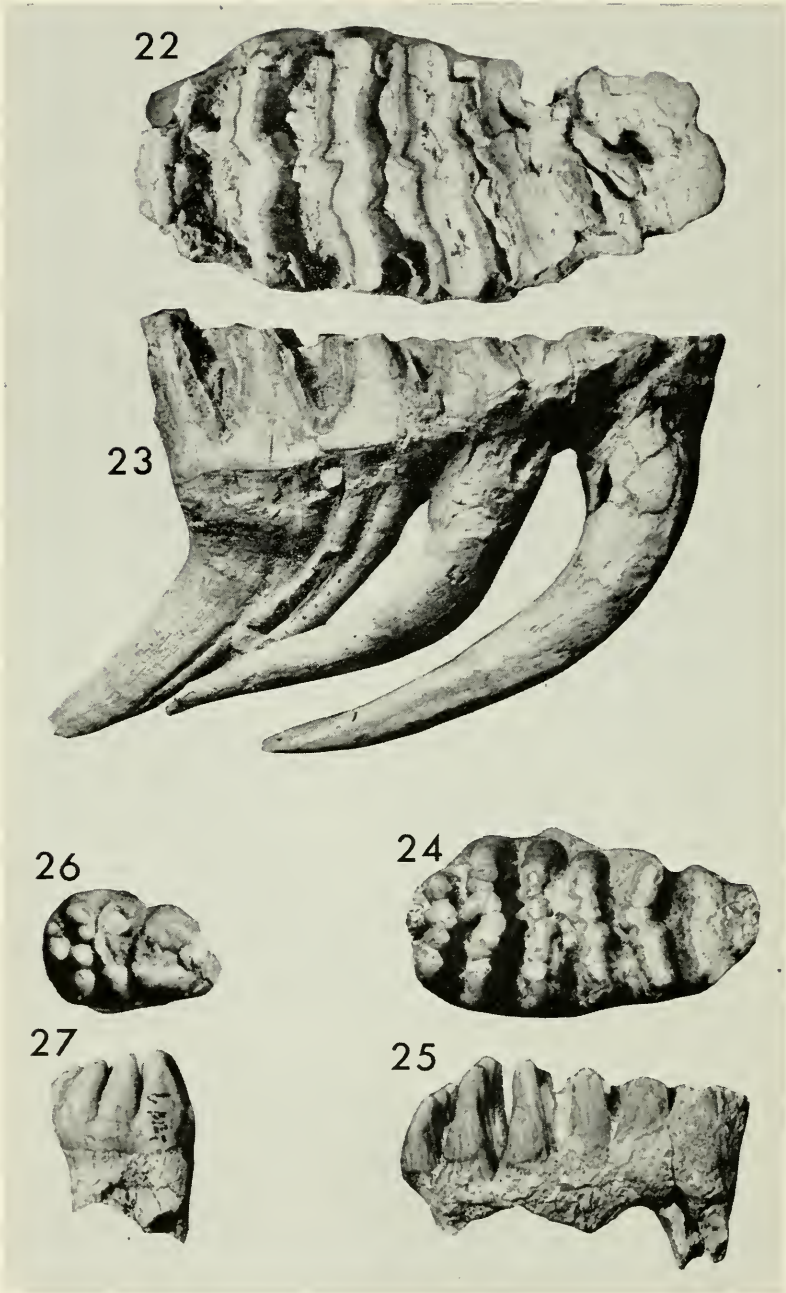
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Plate VI

22. *Loxodonta* sp., IPUB 5828, l.M_1; occlusal view. × 1/2.
23. *Loxodonta* sp., IPUB 5828, l.M_1; lingual view. × 1/2.
24. *Loxodonta* sp., IPUB 5883, l.dM_3; occlusal view. × 2/3.
25. *Loxodonta* sp., IPUB 5883, l.dM_3; lingual view. × 2/3.
26. *Loxodonta* sp., IPUB 5837M, r.dM_2; occlusal view. × 1.
27. *Loxodonta* sp., IPUB 5837M, r.dM_2; buccal view. × 1.

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LOWER VERTEBRATES FROM THE LATE CRETACEOUS HELL CREEK FORMATION, McCONE COUNTY, MONTANA[1]

Richard Estes, Paul Berberian, and Charles A. M. Meszoely[2]

ABSTRACT. Fifty-five lower vertebrate species are recorded from the Upper Cretaceous Bug Creek Anthills locality, Hell Creek Formation, McCone County, Montana. This faunal list closely resembles that from the Lance Formation of Wyoming, also of late Cretaceous age (Estes, 1964). In spite of this general similarity, a number of species are present at Bug Creek Anthills that are absent from the Lance Formation sample: Cf. *Paralbula casei* (Albuloidei; Phyllodontidae), *Palaeolabrus montanensis* (Amiiformes?; Palaeolabridae), *Proamphiuma cretacea* (Caudata; Amphiumidae), an unidentified discoglossid frog, an undescribed baenid turtle, *Adocus* sp. (Testudinata; Dermatemydidae), *Peneteius aquilonius* (Sauria; Teiidae), and an unidentified boid snake.

Both Bug Creek Anthills and the Lance localities are in the upper third of Hell Creek and Lance Formation sections, respectively. A similar flood-plain-riparian association of freshwater and terrestrial forms occurs in both areas, including hybodontid, pristid, and dasyatid sharks; sturgeons and paddlefish; amiid, albulid, and sciaenid fishes; six genera of salamanders; four genera of frogs; seven genera of turtles; eleven genera of lizards; two genera of snakes; two genera of crocodilians; and eight genera of dinosaurs. Slight climatic, ecological, and geographical differences are probably responsible for the minor differences between Lance and Hell Creek faunas; that from the Bug Creek Anthills locality is not notably more advanced in character than that from the Lance.

INTRODUCTION

In the summers of 1962, 1963, and 1964, Robert E. Sloan and his associates at the University of Minnesota collected a series of samples of vertebrate fossils at and near Bug Creek, McCone County, Montana, in the late Cretaceous Hell Creek Formation. The richest of these localities, Bug Creek Anthills, has yielded an extraordinary sample of disarticulated fossil vertebrate material

[1] Fossil vertebrates from the late Cretaceous Hell Creek Formation, Montana: Contribution No. 8.

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(Sloan and Van Valen, 1965; Estes, 1965, 1969d-h; Estes and Berberian, 1969). In the next paper in this series (Estes and Berberian, in press), paleoecological techniques developed by Shotwell (1955, 1958) will be applied to the MCZ sample from Bug Creek Anthills; we here provide only an annotated faunal list of the lower vertebrates at this locality (for collections used, see Acknowledgments). A few taxa present locally in localities at or above the Bug Creek Anthills level (noted in the text) are also included, and a complete list of known Hell Creek Formation vertebrates will be included in Estes and Berberian (in press).

Since many thousands of specimens have been recovered, the individual bones and their frequency of occurrence are not listed in the systematic section. Minimum numbers of individuals and relative abundance of species are given in Table 1; similar data are also given for the Lance Formation, for comparison.

ANNOTATED LIST OF LOWER VERTEBRATES

The faunal list from Bug Creek Anthills is very similar to that described from the Lance Formation of Wyoming (Estes, 1964), as shown in Table 1, and a similar floodplain-riparian environment of deposition and rather similar climatic conditions are indicated. The two local faunas show the same relative abundance of most forms, thus indicating, to a certain degree, that the samples probably reflect actual abundance. Therefore, only those comments supplementing or modifying conclusions reached by Estes (1964) appear here. A detailed paleoecological analysis and comparison of the Bug Creek Anthills and Lance local faunas will appear in Estes and Berberian (in press).

TABLE 1

Minimum number of individuals and relative abundance of lower vertebrates in two localities.

Lower vertebrates	Lance Formation (V5620)		Hell Creek Formation (Bug Creek Anthills)	
	MNI	RA	MNI**	RA
Lonchidion	4	1.0	1	.3
Myledaphus	1	.2	1	.3
Squatirhina	1	.2	X	X
Ischyrhiza	1	.2	X	X
Acipenser	1	.2	7	1.8
Paleopsephurus	1*	.2	3	.5
"Protamia"	1	.2	1	.3
Amia	103	21.0	94	19.4
Belonostomus	5	1.0	1	.3

Lepisosteus	7	1.4	25	5.5
Coriops	26	4.5	3	.5
cf. Paralbula	X	X	1	.3
Palaeolabrus	X	X	7	1.6
Elopidae	1	.2	1	.3
Platacodon	42	8.2	2	.4
Habrosaurus	73	14.1	9	1.8
Opisthotriton	41	8.0	107	22.9
Scapherpeton	22	4.2	61	14.4
Lisserpeton	1*	.2	72	12.8
Prodesmodon	11	2.2	2	.4
Proamphiuma	X	X	2	.4
Scotiophryne	1*	.2	6	1.2
cf. Barbourula	1	.2	1	.3
other frogs	12	2.4	3	.5
Adocus	X	X	1	.3
Basilemys	1	.2	X	X
Compsemys	1	.2	1	.3
Trionyx	1	.2	1	.3
Eubaena	1	.2	3	.5
other baenids	1	.2	4	.8
Emydinae	1	.2	3	.5
Brachychampsa	1	.2	1	.3
Leidyosuchus	1	.2	1	.3
Champsosaurus	1	.2	2	.4
dinosaurs	8	1.6	7	1.8
Peneteius	X	X	1	.3
Chamops	15	3.0	3	.5
Meniscognathus	15	3.0	X	X
Leptochamops	15	3.0	1	.3
Haptosphenus	3	.5	1	.3
Contogenys	X	X	4	.8
Sauriscus	4	.8	X	X
Exostinus	4	.7	3	.5
cf. Gerrhonotus	3	.6	X	X
Pancelosaurus	20	4.0	15	3.2
Parasaniwa	36	7.0	1	.3
Paraderma	2	.4	1	.3
Palaeosaniwa	1	.2	1	.3
Colpodontosaurus	2	.4	3	.5
Litakis	1	.2	X	X
Cuttysarkus	13	2.5	2	.4
Coniophis	1	.2	1	.3
boid snake	X	X	1	.3
?Pterosauria	1	.2	X	X
Total	509	100.0	472	100.0

*Additions since Estes, 1964, Table 5.
**Only MCZ sample used in this calculation.

CLASS CHONDRICHTHYES
ORDER SELACHII
Family Hybodontidae
Lonchidion selachos Estes, 1964

MCZ 9330, teeth and cephalic spines, resemble those figured by Estes (1964, figs. 1, 2d, 3a-b, d) from the Lance Formation of Wyoming. None of the tricuspid teeth with squatinoid roots interpreted by Estes (1964, figs. 2a-c, 3c) as anterior or symphysial teeth occur in the Bug Creek sample. Patterson (1966, p. 331), in describing Jurassic and Cretaceous English species of this genus, suggested that these tricuspid teeth belonged either to *Squatirhina americana* or to an undescribed taxon. The preservation and appearance of the tricuspid Lance teeth indicate that they belong to a squatinoid other than *Squatirhina*. Patterson (1966, p. 326) has referred tricuspid teeth (presumed symphysial teeth) to his Jurassic species *L. heterodon,* but no root structure is known. As he says (1966, p. 331), it is possible that *Lonchidion,* like *Heterodontus,* developed anterior tricuspid teeth with squatinoid roots, but we agree with him that the Lance tricuspid teeth do not belong to *Lonchidion.*

ORDER BATOIDEA
Family Pristidae
Ischyrhiza avonicola Estes, 1964

Only one specimen of this species is represented; it is American Museum of Natural History 9330, from the Harbicht Hill locality, which is about the same stratigraphic level as Bug Creek Anthills and about twenty miles away. Both Bug Creek Anthills and Harbicht Hill are termed transitional or ". . . of Paleocene aspect . . ." by Sloan and Van Valen (1965).

The specimen is 5.0 mm long, its crown flattened and keeled anteroposteriorly. The base is extensively and evenly eroded; the etched appearance suggests that it may have been of coprolitic origin (Fig. 1a-b).

Ischyrhiza avonicola is recorded from the Cretaceous and Paleocene of Texas by Slaughter and Steiner (1968), who note that it seems distinct from larger species of *Ischyrhiza* and *Onchosaurus* and is therefore unlikely to represent young of such larger forms. They have also noted a possible Turonian-Paleocene size increase in *I. avonicola.* The Paleocene Kinkaid Formation specimen figured by Slaughter and Steiner (1968, fig. 3m) is about 3.5 mm

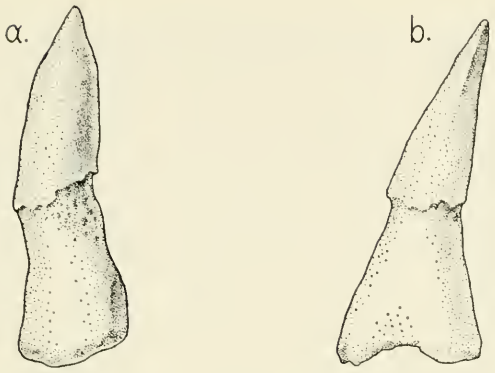

FIG. 1. *Ischyrhiza avonicola,* AMNH 9330, rostral tooth; *a,* dorsal, and *b,* anterior views; Harbicht Hill, Hell Creek Formation, McCone County, Montana; × 8.

long, which is about maximum size of Lance Formation specimens (Estes, 1964, p. 14). They state (1968, p. 237) that their Turonian Eagle Ford Formation specimens are smaller than those from the Lance Formation and the one they figure (1968, fig. 3k) is about 1.8 mm long, not significantly smaller than the minimum 2.0 mm of Lance specimens. Their figure 3k-m, offered as a temporal sequence of size change, thus represents approximately the size variation occurring within Lance Formation specimens, although they state (1968, p. 236) that the ". . . size of the teeth in the Lance collections is very constant . . ." Since they do not give size range for any of their samples, it is difficult to know in what part of the observed range their figured specimens fall. However, the Harbicht Hill specimen is 5.0 mm in total length, significantly exceeding the known range of Lance specimens. The crown of the Harbicht Hill specimen is longer relative to the base than in other specimens of this species, but this condition is partly the result of erosion. In other features it does not differ from *I. avonicola* and can be referred to it without much doubt. A late Paleocene specimen from Wyoming (Shotgun member, Fort Union Formation, specimens collected by Craig Wood) is 3.9 mm long. This specimen and that from Harbicht Hill may provide substantiation for Slaughter and Steiner's suggestion of temporal size increase in *I. avonicola,* and may also strengthen the "Paleocene aspect" of the Harbicht Hill locality suggested by Sloan and Van Valen (1965).

Family Dasyatidae

Myledaphus bipartitus Cope, 1876

MCZ 9331, isolated teeth and dermal denticles, closely resemble specimens figured by Estes (1964, figs. 7, 8d). As indicated by Estes, *Myledaphus* is close to the African late Cretaceous *Parapalaeobates*. Specimens of the latter figured by Stromer and Weiler (1930, pl. II, fig. 15; incorrectly cited by Estes, 1964, p. 18, as 1913) show a crown pattern coarser than but essentially identical to that of *Myledaphus*, having the same transverse ridge separating anterior and posterior grinding surfaces. In view of the great similarities between teeth of *Parapalaeobates* and *Myledaphus*, no more than specific difference between them is justified. Although histological comparison has not yet been made, we doubt that differences supporting generic separation could be found; we therefore suggest (1) that *Parapalaeobates* be considered a junior synonym of *Myledaphus*, thus extending the range of the latter genus to the Upper Cretaceous of North Africa, and (2) that *M. pygmaeus* be separated from *M. bipartitus* by its relatively coarser sculpture and more flattened, rounded crown. In spite of the name, the teeth of *M. pygmaeus* are as large as the largest specimens of *M. bipartitus*.

CLASS OSTEICHTHYES

ORDER ACIPENSERIFORMES

Family Acipenseridae

Acipenser eruciferus Cope, 1876

MCZ 9433-9442, 9448-9450. Fragmentary pectoral spines, cleithra, clavicles, supracleithra, pterotics, dermosphenotics, supraorbitals, (?) dermosupraoccipitals, (?) parietals, hyoid elements, ventral precaudal scute, and dermal scutes have been recovered; terminology of Gregory (1933) for the dermal bones is followed. The dermal sculpture of specimens that possess it is varied; pustular, ridge-and-valley, and pitted types occur, depending on element and size, but a latticelike pattern occurs on most specimens. The sculpture is fine in small specimens, much coarser in larger ones. Many *Acipenser*-like lateral scutes occur (Estes, 1964, fig. 11a; Lambe, 1902, pl. 21). Such scutes also appear in living *Scaphirhynchus*, although scute sculpture is less coarse than in *Acipenser*, at least in our comparative material. Many tiny, comb like scutes like those covering the body of Recent examples of both genera

occur also (Fig. 2c); these are vertically elongated rather than expanded and flattened like polyodontid scutes, but resemble them to some degree (Fig. 2j-k).

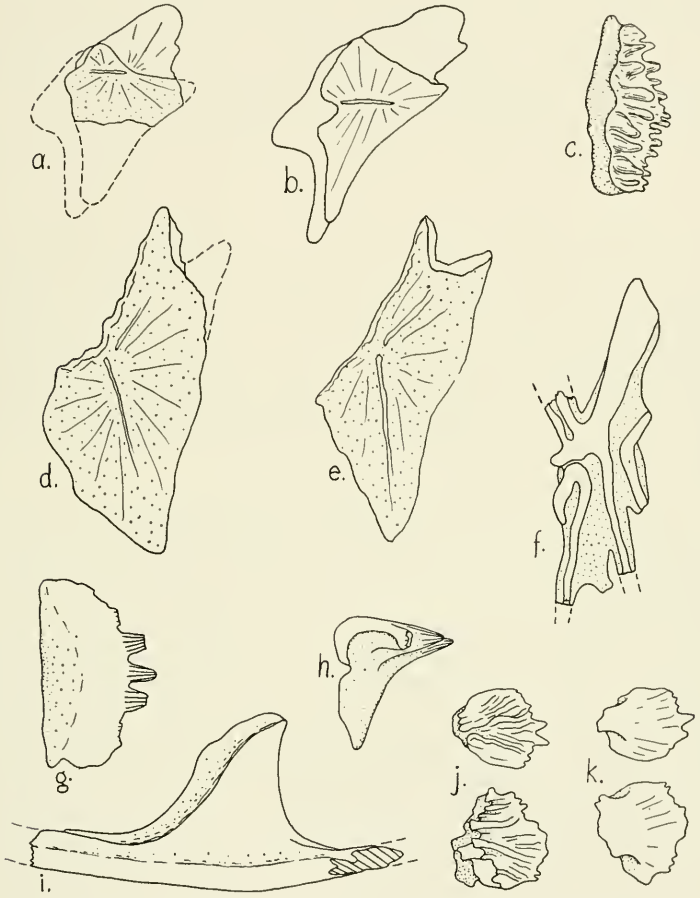

FIG. 2. a, *Acipenser eruciferus*, restored right supracleithrum, MCZ 9450, × 1; *b*, Recent *Acipenser* sp., the same, × 0.5; *c*, *A. eruciferus*, dermal scute, MCZ 9442; *d*, the same, left clavicle, MCZ 9448, × 1.8; *e*, Recent *Acipenser* sp., the same, × 0.5; f-k, *Paleopsephurus wilsoni*, *f*, rostral(?) scute, MCZ 9446, × 1.8; *g*, outer, and *h*, dorsal views of referred dermal denticle, MCZ 9445, × 3; *i*, dorsal view of left maxilla, MCZ 9332, × 3; *j*, outer, and *k*, inner views of two dermal denticles, MCZ 9445, × 3; *a*, *c-d*, *f-k* from Bug Creek Anthills, Hell Creek Formation, McCone County, Montana. Sculpture pattern indicated by coarse stipple on *a-b*, *d-e*.

The shoulder girdle elements resemble those of *Acipenser* more than those of *Scaphirhynchus*. The cleithrum is a powerful element with a complexly curved attachment area for the pectoral spine and fin. The area of dermal bone separating adductor attachment from pectoral spine articulation is of relatively greater anteroposterior extent than it is in Recent *Acipenser*, and this condition seems to be true of the plate-like ventral expansion as well. In other respects the specimens match those of Recent *Acipenser*.

The clavicle closely resembles that of Recent *Acipenser* (Fig. 2d).

The supracleithrum differs from that of *Acipenser* in having the dermal ridge closer to the unsculptured suprascapular-extrascapular articulation surface(Fig. 2a); one (or both) of the latter two bones evidently extended over relatively more of the supracleithrum than it did in Recent *Acipenser*.

Pectoral spine fragments are as in Lance Formation specimens: coarsely grooved longitudinally, expanded proximally, and subtriangular in cross-section. Cross-section of all fin spines is compressed as in Oldman Formation *A. albertensis* (see Estes, 1964, fig. 11b, and pp. 21-22).

Preserved hyoid bones are mostly ceratohyals. In robust development and widely-flared ends, they closely resemble those of *Acipenser*. The hollow, unossified ends show numerous transverse growth rings.

Dermal roofing bones are all fragmentary and generally undiagnostic. Parietals, dermosupraoccipitals, and operculum are referred on general resemblance to these same rather featureless bones in *Acipenser*, and some may be misidentified. Dermosphenotic and supraorbital fragments are characteristic but are too broken for discussion. The pterotics have a posteroventral (hyomandibular-intercalary) ridge that ends centrally rather than continuing two-thirds of the way forward as in living *Acipenser*.

The type of *Acipenser eruciferus* is a fragment of dermal roofing bone from the Lance Formation that Cope (1876) believed to be a lungfish tooth plate. Estes (1964) referred similar Lance Formation material to *Acipenser*, as *A. eruciferus* (Cope), although the type is a *nomen vanum*. No nomenclatorial difficulties should be encountered unless articulated material should show that more than one species of *Acipenser* is present in the Lance Formation and that they are indistinguishable on the basis of dermal scute sculpture. In identifying material from other deposits, use of the name

A. cruciferus is less assured, yet the close temporal and geographical association of Lance and Hell Creek Formations lends some security to the reference. We prefer to continue using this name since the only other described species from the midcontinent is *A. albertensis* (Lambe, 1902), itself a *nomen nudum* based only on dermal scutes from the Campanian Oldman Formation of Alberta that are inseparable from those of *A. cruciferus*.

The Hell Creek specimens referred to *Rhineastes* sp. by Brown (1907, p. 842) are actually referable to *Acipenser cruciferus* (Estes, 1964, p. 21).

Protoscaphirhynchus squamosus Wilimovsky, 1956

This poorly known acipenserid was described from the same locality in the Fort Peck region that produced *Paleopsephurus wilsoni* (Wilimovsky, 1956). It is thus high in the Hell Creek Formation section, perhaps at Harbicht Hill level or higher (Sloan and Van Valen, 1965, fig. 1). No specimens referable to this form have been identified at Bug Creek Anthills.

Family Polyodontidae

Paleopsephurus wilsoni MacAlpin, 1947

MCZ 9332, 9443-9447, maxillae, pterotics, frontal, rostral dermal scutes, and dermal denticles have been identified. The maxillae are distinctive bones, being flat externally and all bearing a prominent ectopterygoid process grooved dorsomedially (Fig. 2i). All five specimens are broken at both ends but direct comparison with the type specimen makes the identification clear. MacAlpin (1947) noted that the ectopterygoid process was present as a thin process in *Psephurus* and that a similar process was also present in *Saurichthys* and *Elonichthys*. Woodward (1895, pl. 1, fig. 3) figures an almost exactly similar process in *Chondrosteus* that was not noted by MacAlpin.

Frontal and pterotic match comparable elements in *Paleopsephurus*. Dermal sculpture on the frontal is much more prominent than on the pterotic. Both degrees of sculpture development occur on various parts of the type specimen and the variation is probably not significant.

Some dermal scutes are elongated, stellate, coarsely ridged, and thickened dorsally (Fig. 2f). We interpret these as rostral scutes because of their similarity to those of Recent paddlefish; they differ from the latter in being relatively less stellate, more robust, and

more anteroposteriorly elongated. These differences may indicate a rostrum proportioned more as in *Polyodon* than in *Psephurus.*

Trunk dermal denticles differ from those figured by MacAlpin in being flat-topped, and in having an attachment process almost at right angles to the body of the scute (Fig. 2j-k). Scute surfaces are coarsely striated and grooved, and the posterior borders are denticulated. One larger, less expanded scute (Fig 2g-h) may be from near the shoulder girdle. Among scutes figured by MacAlpin (1947), those of *Crossopholis* are most like the Bug Creek specimens, but polyodontid dermal scute variability is great, and the total range is not known for *Paleopsephurus,* so that the variation may not be significant.

ORDER ASPIDORHYNCHIFORMES
Family Aspidorhynchidae
Belonostomus longirostris (Lambe, 1902)

MCZ 9333, a fragmentary predentary and a skull fragment, resemble Lance Formation specimens (Estes, 1964, p. 22).

ORDER AMIIFORMES
Family Amiidae
Amia fragosa (Jordan, 1927)

Large numbers of specimens of this species have been recovered (MCZ 9286-9293, 9390-9432), and have been reviewed by Estes and Berberian (1969), who substantiated Janot's (1967) suggestion that *Kindleia* is a synonym of *Amia.*

Amia ("Protamia") sp.

Two glassy, translucent tooth tips (MCZ 9334) are similar to those of Lance Formation specimens. No vertebrae or large skull elements occur in the large Bug Creek sample. Janot (1967) has suggested that *Protamia,* like *Kindleia,* is a synonym of *Amia.*

The presence of both small and large amiids is common in many late Mesozoic and early Cenozoic deposits both in Europe and in North America (Estes, 1964); careful study of this material would be of considerable systematic and zoogeographic interest.

ORDER AMIIFORMES?
Family Palaeolabridae
Palaeolabrus montanensis Estes, 1969h

This fish was described by Estes (1969h) on the basis of palatal tooth plates, skull and mandibular elements, and vertebrae. The

type species is from the late Paleocene or early Eocene Dormaal deposits in Belgium (Casier, 1967).

ORDER LEPISOSTEIFORMES
Family Lepisosteidae
Lepisosteus occidentalis Leidy, 1856

Almost all bones of skull and skeleton are present (MCZ 9354-9389).

Estes (1964) gave a restoration of this species, which is a wide-snouted form closely related to the living alligator gar *L. spatula.* The quadratojugal, found at Bug Creek but not in the Lance Formation sample, does not differ fundamentally from the same bone in *Lepisosteus spatula.*

The circumorbital series (incomplete in the Lance Formation sample) has been identified and shows no significant differences from that of Recent *Lepisosteus.*

ORDER ELOPIFORMES
SUBORDER ELOPOIDEI
Family Elopidae

Estes (1964, p. 48, fig. 23) described large teleost scales having a granular apical sculpture as resembling those of the late Cretaceous elopid *Dinelops,* from the English Chalk. Casier (1966, p. 133, pl. 13. fig. 3) described similar scales from the Eocene London Clay and referred them to an unknown elopid. Two scale fragments (MCZ 9338) are identical to the Lance Formation specimens but do not suggest any further clues as to the generic identity of the fish.

SUBORDER ALBULOIDEI
Family Phyllodontidae
cf. Paralbula casei Estes, 1969a

MCZ 9335 consists of three teeth, two of which are superimposed phyllodont teeth; the other is a single tooth with the characteristic coarse tooth pattern of *Paralbula casei* (Estes, 1969a). The directly successional rather than the overlapped arrangement of the teeth indicates a phyllodontine rather than a paralbuline replacement (Estes, 1969a), but an occasional directly successional pair of teeth may occur in the latter group. The coarse surface sculpture and appearance of the isolated tooth are as in the type of *P. casei* (Estes, 1969a, fig. 3). *P. casei* is known from the Campanian of

Wyoming, Maestrichtian of New Jersey, and Eocene of England; this record constitutes the highest stratigraphic occurrence of the species in the Western Interior region of North America.

Family Albulidae
Coriops annicolus Estes, 1969h

These albuloid parasphenoid and basibranchial tooth plates (MCZ 9340) differ from those of *Albula* in having the teeth fused to the plates and in lacking otic articulation surfaces on the parasphenoid. *Coriops* also occurs in the Lance Formation (Estes, 1969h).

ORDER PERCIFORMES
Family Sciaenidae
Platacodon nanus Marsh, 1889

MCZ 9336, two fifth ceratobranchials; MCZ 9337, referred dentaries, maxillae, vertebrae, and other bones.

The fifth ceratobranchials are paired and have the characteristic tooth arrangement of this species as indicated by attachment areas (Estes, 1964, p. 51, fig. 25) although no teeth are preserved on these specimens. Referred skull elements, vertebrae, and spiny rays may belong to this species or may include other perciform types as well.

Teleostei *incertae sedis*

Numerous vertebrae and miscellaneous fragments of skull bones may indicate teleosts other than the five noted above, but they are not distinctive enough for identification.

CLASS AMPHIBIA
ORDER CAUDATA
SUBORDER AMBYSTOMATOIDEA
Family Scapherpetontidae
Scapherpeton tectum Cope, 1876

MCZ 3673. Vertebrae, atlantes, dentaries, maxillae, parietals, postdentary "compound" bones, and exoccipitals are preserved. Estes (1969b) referred both this genus and *Lisserpeton* to the Ambystomatoidea on the basis of fused postdentary "compound" bones, including fused prearticular and angular.

Lisserpeton bairdi Estes, 1965

MCZ 3674, 3677-3679. Vertebrae, atlantes, dentaries, maxillae, parietals, postdentary "compound" bones, and exoccipitals are preserved. Figures and descriptions of this relative of *Scapherpeton* are given in Estes (1965).

Family Prosirenidae
Prodesmodon copei Estes, 1964

MCZ 3652, trunk vertebrae, are rare at Bug Creek Anthills, much rarer than in the Lance Formation. Reasons for referring this genus to the Prosirenidae are given in Estes (1969c).

Family Batrachosauroididae
Opisthotriton kayi Auffenberg, 1961

MCZ 3676. Vertebrae, atlantes, dentaries, exoccipitals, parietals, premaxillae, and maxillae have been identified. Reasons for referring this genus to the Batrachosauroididae are given in Estes (1969b).

SUBORDER SALAMANDROIDEA?
Family Amphiumidae
Proamphiuma cretacea Estes, 1969e

This earliest amphiumid, represented only by vertebrae, has been described by Estes (1969e) from Bug Creek Anthills. It is probably ancestral to the Recent *Amphiuma*.

SUBORDER MEANTES
Family Sirenidae
Habrosaurus dilatus Gilmore, 1928

MCZ 3675. Vertebrae, atlantes, and dentaries are present, and are similar to Lance Formation specimens.

ORDER SALIENTIA
Family Discoglossidae
Scotiophryne pustulosa Estes, 1969f

This frog was described by Estes (1969f) on the basis of ilia, humeri, maxillae, and squamosals; the Recent Eurasian genus *Bombina* appears to be its closest relative.

cf. *Barbourula* sp.

MCZ 3653, a single right ilium, has a relatively large acetabular fossa with a prominent flare of the anterior border and a prominent iliac symphysis, as noted by Estes (1964, p. 55, fig. 56) in the Lance Formation specimens. Material described but not named by Hecht and Hoffstetter (1962) indicates that a European early Oligocene discoglossid also displays these characteristics. The European ilia are similar to Lance and Bug Creek specimens and may perhaps be placed in the same genus, which will be described in a paper now in preparation by Hecht and Hoffstetter.

Undescribed genus and species

Distinctive humeri known from only two specimens (MCZ 3654) have raised olecranon scars of rather limited proximal extent that are sharply demarcated by concave areas on either side. The humeral ball is relatively large and projects in lateral view. The medial epicondyle is blunt and is broken on both specimens; the lateral epicondyle is essentially undeveloped (Fig. 3).

These unusual humeri are referred to the Discoglossidae on the basis of the blunt, truncated medial epicondyle, the large and projecting ball, and the limited extent of the olecranon scar; these conditions resemble those of *Alytes,* an essentially fossorial discoglossid. Somewhat similar conditions also prevail in *Rhinophrynus,* also a burrower, although the detailed resemblance is with *Alytes.* Humeri referred to *Scotiophryne* are quite different (Estes, 1969f, fig. 3), and because of both the dissimilarity of the humeri and the very different adaptations in the Recent genera, it seems unlikely that the *Barbourula*-like ilium and these *Alytes*-like humeri are from the same taxon. The Bug Creek humeri are distinctive, but we can offer no further comment on their relationships at this time.

Family Pelobatidae?
Eopelobates sp. ?

Material questionably referred to the Pelobatidae by Estes (1964, figs. 30, 31c-e) and other specimens placed "near Hylidae?" (1964, fig. 31a-b) are perhaps referable to a primitive species of *Eopelobates* on the basis of squamosal shape and sculpture similarities to a new Eocene pelobatid from North America (Estes, 1970, in press). Bug Creek material (MCZ 3655) includes several fragmentary maxillae, one fragmentary squamosal, and

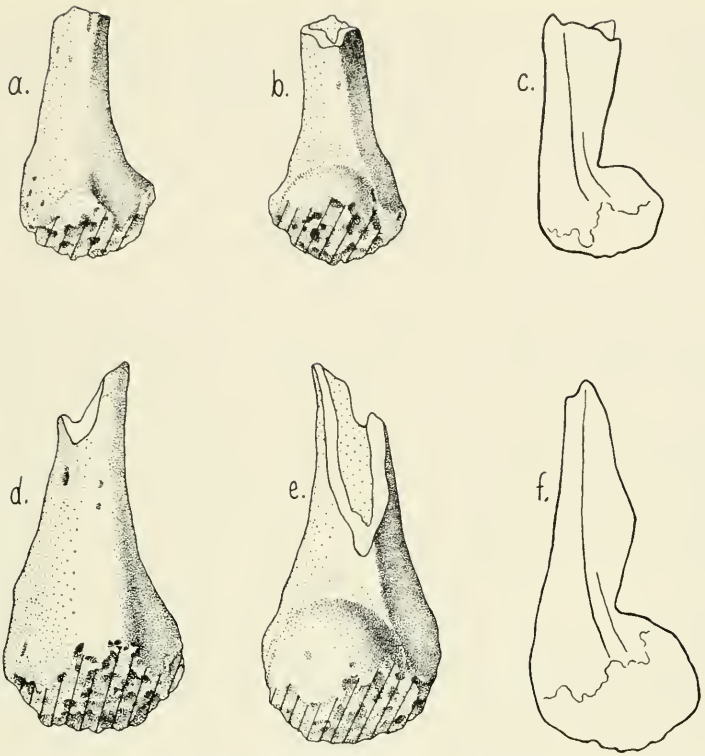

FIG. 3. Right humeri of undescribed genus and species of discoglossid; *a-c,* dorsal, ventral and anterior (outline) views of MCZ 3654a; *d-f,* the same, MCZ 3654b; Bug Creek Anthills, Hell Creek Formation, McCone County, Montana; × 8; cross-hatching indicates broken surface.

three ilia, all similar to the Lance Formation specimens. No further comment on these specimens is possible at this time.

Other Frog Remains

(1) Two maxillary fragments that lack external sculpture, have posterior processes indicating the presence of a complete maxillary arcade, and have teeth set in a relatively deep sulcus dentalis; (2) two humeri with medial, symmetrical olecranon scars that are of a type common in many of the advanced frog families; (3) one procoelous vertebra and two other badly worn and abraded frog vertebrae that are the only axial frog elements in the Bug Creek

sample; (4) a heavily worn and broken ilium with a well-defined dorsal crest that is of a type seen in several frog families; (5) three postdentary lower jaw fragments, two proximal radioulna fragments, and a badly broken tibiofibula that are distinctively anuran but have no special identifying features.

ORDER TESTUDINATA

Family Baenidae

Eubaena cephalica Hay, 1908

A nearly complete skull, fractured on the supraoccipital crest and missing the right maxillary area, is present, along with isolated cranial and mandibular elements (MCZ 3510-3512, 3519, 3530). This is the second known skull referable to this species, and it closely resembles the type from the Lance Formation of Wyoming. The skull referred to *E. cephalica* by Estes (1964, p. 97) belongs to undescribed genus 1 noted below. A revision of the baenid turtles is now being made by Eugene Gaffney, and further comment on these specimens will appear there.

Undescribed genus and species 1

Disarticulated skull elements (MCZ 3514) and shell fragments are referable to a distinctive new baenid genus, and will be described in a forthcoming study by Eugene Gaffney.

Undescribed genus and species 2

Another new genus of baenid turtle occurs in the Bug Creek sample and is represented only by isolated maxillae (MCZ 3515-3518). It differs from both *Eubaena* and the other undescribed baenid in having an exceptionally wide maxillary triturating surface without a ridge. These specimens will also be described by Eugene Gaffney, on the basis of more complete material from the Paleocene of Wyoming.

Family Dermatemydidae

Compsemys victa Leidy, 1856

MCZ 3671, numerous shell fragments, have the characteristic sculpture pattern of many closely-set, flat-topped pustulae seen in all described species of this genus. *C. victa* occurs in the Lance Formation of Wyoming, and the Bug Creek specimens probably belong to this species.

Adocus sp.

The Bug Creek specimens referred here all have a very fine sculpture (about eight to ten pits per cm) as in some species of *Adocus* (Gilmore, 1919). Brown (1907; p. 842) originally identified Hell Creek specimens as *A. lineolatus,* but Gilmore indicated (1919), p. 25 and other papers) that specific identification cannot be determined by sculpture pattern. In the late Cretaceous, two types of *Adocus* sculpture occur, however: a very fine type with eight to ten pits per cm, and a more well-defined type with six to seven pits. All Hell Creek Formation specimens are in the former group suggesting that these two sculpture types are not simply variants from different shell areas. Lance Formation specimens are clearly referable to *Basilemys* (Estes, 1964), having coarse sculpture with only three to four pits per cm.

Because too few specimens of *Adocus* are known, the validity of the described species cannot be assessed at this time, but it is safe to say that more are named than is justified by the material. *Basilemys* and *Adocus* are probably quite closely related (as compared with other fossil so-called dermatemydids). *Adocus* is limited to the Maestrichtian and occurs on the East Coast as well as in the Western Interior. It is primitive in having inframarginal shields and unexpanded pectoral shields. *Basilemys,* which extends through both Campanian and Maestrichtian stages, has not gone as far as *Adocus* in neural and suprapygal reduction. The two genera seem to be distinct (Table 2) and probably had a common ancestor in pre-Campanian time.

TABLE 2

Comparison of characters separating *Adocus* and *Basilemys*

Adocus	*Basilemys*
1. Inframarginals large, extending across bridge.	1. Tiny axillary and inguinal inframarginals (except *B. nobilis).*
2. A single suprapygal; posterior neurals reduced.	2. Two or three suprapygals; posterior neurals unreduced (except *B. nobilis?)*
3. Posterior marginal shields large, elongated anteroposteriorly.	3. Posterior marginal shields narrow, elongated mediolaterally.
4. Plastral lobes rounded.	4. Plastral lobes tend to be acute.

5. Pectoral shields little expanded medially.	5. Pectoral shields greatly expanded medially.
6. Sculpture relatively smooth and fine, about six to ten pits per cm.	6. Sculpture relatively rough and coarse; about three to four pits per cm.
7. Carapace length 480-670 mm.	7. Carapace length 690-940 mm.

Family Testudinidae
Subfamily Emydinae?
Unidentified genus and species

Fragmentary eighth cervical vertebrae (MCZ 3567-3568, 3573) have a double concave articulation surface posteriorly. Numerous fragments of peripherals (MCZ 3656) and costals (MCZ 3657) show deeply impressed shield sulci and marked changes in elevation between the shield areas.

Double, concave articulation surfaces on the eighth cervical vertebra are known only in the Testudinidae (Williams, 1950). The fragments of carapace and plastron closely resemble the shells of pond turtles, especially *Pseudemys*. The questionable family reference given by Estes (1964, p. 99) to similar specimens from the Lance Formation is confirmed by the distinctive cervical vertebrae present here. This is the earliest record of the family, otherwise not known before the Eocene *Echmatemys;* it will be discussed further in a study in preparation.

Family Trionychidae
Trionyx sp.

A partial left hypoplastron (MCZ 3658) and many costal and neural fragments (MCZ 3672) all bear a characteristic trionychid sculpture. The hypoplastron shows that the plastron was reduced, indicating that the specimen cannot be referred to the line of fossil trionychids often designated as *Plastomenus*. The presence or absence of a prenuchal bone cannot be demonstrated in this material, but recent work (Webb, 1962) indicates that the presence of a prenuchal is insufficient ground for separating the genus *Aspideretes*. It thus seems best to refer this material to *Trionyx* (s. l.) as well as the material referred to *Aspideretes beecheri* by Estes (1964).

CLASS REPTILIA
ORDER EOSUCHIA
Family Champsosauridae
Champsosaurus sp.

MCZ 3651, ten vertebrae, a few tooth crowns, and three ribs are present. The specimens are clearly referable to this genus but are specifically indeterminable. *Champsosaurus* was evidently rare at Bug Creek Anthills, and is represented only by small individuals.

ORDER SAURIA
SUBORDER SCINCOMORPHA
Family Teiidae
Chamops segnis Marsh, 1892

MCZ 3659, dentary fragments, fragment of left maxilla, four unnumbered tooth-bearing fragments; MCZ 3660, fragmentary parietals. These specimens were originally cited by Estes (1964, p. 108) as possibly forming a new species of *Chamops* because Bug Creek specimens available at that time all seemed to show less bulbous tooth bases than did Lance Formation fossils. Subsequently collected Bug Creek specimens do not bear out this distinction. *Chamops* most closely resembles the Recent South American species *Callopistes maculatus* (Estes, 1969d).

Leptochamops denticulatus (Gilmore, 1928)

MCZ 3661, two maxillae and a few tooth-bearing fragments, are poorly preserved but appear to belong to this species.

Haptosphenus placodon Estes, 1964

MCZ 3686, fused right dentary and splenial and a coronoid with adhering parts of fused dentary and surangular are preserved. The dentary shows the short, heavy jaw; short, rather *Chamops*-like teeth; and fused postdentary bones with visible suture lines as in Lance specimens. *Haptosphenus* is aberrant in the fusion of jaw elements; we do not know of a comparable situation in lizards. Nevertheless the closest resemblances of *Haptosphenus* seem to be with *Chamops,* differing from the latter both in bone fusion and in having almost acrodont teeth; it may be an aberrant teiid derived from a *Chamops*-like ancestor.

Peneteius aquilonius Estes, 1969d

This lizard was described by Estes (1969d); it shows resemblances both to the Recent *Teius* and *Dicrodon* as well as to the late Cretaceous *Polyglyphanodon.* The holotype is the unique specimen.

Family Scincidae ?
Contogenys sloani Estes, 1969g

This lizard was described by Estes (1969g). *Contogenys* resembles members of the Scincidae; although it is not clearly referable to that family, it is certainly a member of the Scincoidea.

Family Anguidae
Pancelosaurus piger (Gilmore, 1928)

This species was described in detail and removed from *Peltosaurus* by Meszoely (1970), who, in his revision of the Anguidae, placed *Pancelosaurus* at the base of the subfamily Anguinae rather than in the Gerrhonotinae as suggested by Estes (1964).

Family Xenosauridae
Exostinus lancensis Gilmore, 1928

A number of dentary and maxillary fragments and a referred frontal are present. The jaw elements (MCZ 3662a) do not differ significantly from Lance Formation specimens of this species. The frontal (MCZ 3662b) may be referable to *E. lancensis* on the basis of dermal sculpture pattern. It is eroded, and because of this and its small size, it does not display a sculpture pattern as well developed as that on the larger Lance Formation parietal referred by Estes (1964, pl. 3). If properly referred, frontals were paired in *E. lancensis,* a condition that, while different from that in later species of *Exostinus* and from *Xenosaurus* itself, is not a surprising one in view of its Cretaceous age.

Diploglossa *incertae sedis*
Colpodontosaurus cracens Estes, 1964

Well-worn fragments of dentaries and maxillae (MCZ 3663) lack teeth except in one specimen.

Estes (1964, p. 127) placed *Colpodontosaurus* as Diploglossa *incertae sedis* on the basis of a tiny free ventral border of the intramandibular septum, the presumed lack of jaw hinge, and the

absence of basal fluting on teeth. Teeth on the type specimen have been broken since the original figure (1964, fig. 60) was made, and these fresh break surfaces show an irregular, almost fluted appearance; under high magnification, several faint grooves occur on the teeth of UCMP 49938, a maxilla from the Lance Formation.

Although a tiny free ventral border is present on the intramandibular septum, it is little different from that of *Varanus* and *Parasaniwa*. Reexamination of the type of *Colpodontosaurus* indicates that the presence or absence of a jaw hinge in this specimen cannot be determined, although the dentary seems to have a relatively greater posterior projection than it does in *Parasaniwa*.

On the maxillary fragments, the posterior end shows elongation of the posterior external mental foramina as in *Parasaniwa* and varanids. The dorsal border of the bone is elongated and gently sloping as in *Parasaniwa* and the anguids.

Absence of sculpture, delicate construction, condition of intramandibular septum, and elongated mental foramina are all as in varanids, and the last two characters show parasaniwid resemblances as well. The essential absence of basal infolding of teeth, and the long, slender, posterior process of the maxilla are characters suggesting diploglossans. The latter character is completely unlike that in *Varanus, Saniwa* and parasaniwids in indicating that the tooth row extended posteriorly well under the orbit.

Although new interpretation and new specimens have shown some varanid and parasaniwid characters, there are enough detailed differences to maintain *Colpodontosaurus* as Diploglossa *incertae sedis*.

Family Parasaniwidae

Parasaniwa wyomingensis Gilmore, 1928

A few dentary and maxillary fragments and a parietal (MCZ 3664) show the characteristic simple infolding of tooth bases, fused intramandibular septum and sculptured skull roof of topotypic material from the Lance Formation.

Paraderma bogerti Estes, 1964

A fragmentary left maxilla, an isolated tooth with adherent jaw fragment and two referred vertebrae (MCZ 3687) do not differ from Lance Formation specimens.

INFRAORDER PLATYNOTA
Family Varanidae
Palaeosaniwa, cf. *P. canadensis* Gilmore, 1928

Only a single large varanid vertebra occurs in the Bug Creek sample (MCZ 3665), and it differs from Lance Formation specimens in having less well-developed zygosphenes. The Bug Creek specimen is about the size of the type (from the Campanian Oldman Formation of Canada), and has convex lateral borders of the centrum, as do Eocene *Saniwa* and both Oldman Formation and Lance Formation *Palaeosaniwa.*

ORDER SAURIA ?
Family *incertae sedis*
Cuttysarkus mcnallyi Estes, 1964

Three dentaries (MCZ 3666) show no significant differences from the Lance Formation specimens. The systematic position of this genus is even less clear now than when discussed by Estes (1964). Nearly forty dentaries are known from the Lance Formation type area, but no maxillary fragments of this distinctive animal were discovered.

A number of people have commented on relationships of *Cuttysarkus,* and have offered possibilities spanning all lower vertebrate Classes. One colleague suggested that the name was based on arthropod mandibles, yet we must reject his contribution by noting that *Cuttysarkus* jaws are composed of characteristic, cellular vertebrate bone. One of the most reasonable possibilities came from C. Wilson Kerfoot, who suggested that there were many similarities between the dentaries of *Cuttysarkus* and the salamander *Opisthotriton.* Absence of a sulcus dentalis, lack of definition of Meckelian groove, straight posterior border of the dentary and posteroventral depression lingually are all indicative of salamander dentary structure, although each of these features can be matched in one or another lizard group. The teeth are not pedicellate but this condition can be matched in the salamanders *Prodesmodon* and *Habrosaurus.* The absence of maxillae could be interpreted as evidence that *Cuttysarkus* was a larval salamander. Yet all Lance and Hell Creek Formation salamanders are distinctive, and most are essentially of "larval" or paedomorphic type (Estes, 1964). *Cuttysarkus* jaws are too distinctive themselves, in any case, to be from larvae of any of the salamanders present. In the Lance Formation, each known type of salamander vertebrae

is matched by distinctive skull elements consonant with the vertebrae in size, morphology, state of preservation, and frequency of occurrence. Mandibular elements of *Proamphiuma* (Estes, 1969c) are unknown, but there is no resemblance of *Cuttysarkus* to *Amphiuma* in maxillary structure. *Cuttysarkus* may not be a lizard, but we retain it there for the present.

ORDER SERPENTES
SUPERFAMILY BOOIDEA
Family Aniliidae
Coniophis precedens Marsh, 1892

Only a few vertebrae are present (MCZ 3667) and indicate no difference from Lance Formation specimens (Estes, 1964; Hecht, 1959). A pair of coossified frontals (MCZ 3668) is also referred; no comparisons are made at this time pending study of other *Coniophis* material by Hecht.

Family Boidae
Subfamily Erycinae ?
Unidentified genus and species

A single vertebra (MCZ 3669) is poorly preserved and broken but is of interest in demonstrating the presence of a second species of snake from the Cretaceous of North America (Fig. 4). Centrum length (CL, Auffenberg, 1963, fig. 3) is 8.8 mm, about the size of some Eocene *Boavus* vertebrae but twice as large as the largest known *Coniophis* specimen. In having a condylar ball with rather sessile edges, sessile haemal carina and paradiapophyses, and a compact centrum shape, this specimen resembles vertebrae of the subfamily Erycinae (*sensu* Hoffstetter, 1955) rather than those of the Boinae. Erycines have previously not been reported before the Eocene (Hecht, 1959). Without characters of the neural arch, this specimen cannot be identified more specifically.

ORDER CROCODILIA
SUBORDER EUSUCHIA
Family Crocodylidae
Subfamily Crocodylinae
Leidyosuchus sternbergi Gilmore, 1910

Many crocodile teeth (MCZ 3648) occur in the Bug Creek sample and, on the basis of shape and general appearance, are similar to those of the type specimen and referred Lance Formation material (Estes, 1964).

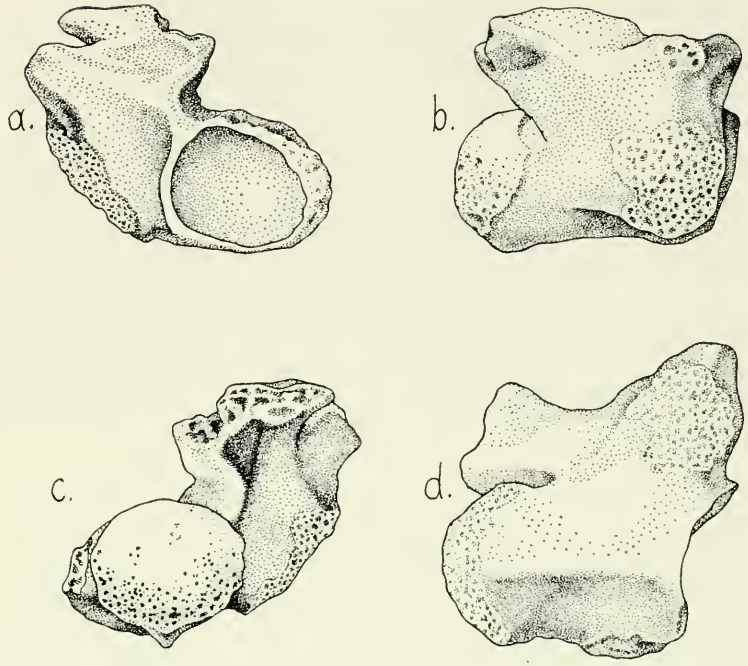

FIG. 4. Vertebra of boid snake, MCZ 3669; *a,* anterior, *b,* lateral, *c,* posterior, and *d,* ventral views; Bug Creek Anthills, Hell Creek Formation, McCone County, Montana; × 4.

Subfamily Alligatorinae
Brachychampsa montana Gilmore, 1911

Bulbous, low-crowned teeth (MCZ 3650), scutes, fragmentary limb, vertebral and skull bones are relatively common. The teeth are relatively smaller than those of the type specimen, which is also from the Hell Creek Formation of Montana. Some of the skull and skeletal fragments referred here probably belong to *Leidyosuchus.*

ORDER SAURISCHIA
SUBORDER THEROPODA
INFRAORDER COELUROSAURIA
Family Coeluridae ?
Unidentified genus and species

These delicate teeth (MCZ 3694) are serrated only on their posterior borders and are rare at Bug Creek Anthills. Estes (1964)

noted that similar Lance teeth with fine serrations resembled those of *Velociraptor,* but in shape and size they resemble those of other coelurids as well, including the Oldman Formation *Chirostenotes* and the Triassic *Coelophysis.* Generic identifications cannot be based on teeth of this sort (Pl. 1b).

Paronychodon lacustris Cope, 1876

A few teeth (MCZ 3645) of this peculiar type occur in the Bug Creek sample (Pl. 1d). *Paronychodon* teeth have been figured several times, most recently by Russell (1935, pl. 2, fig. 8). The flattened lingual side may indicate an anterior tooth; other referred specimens with the same coarse striations (Pl. 1e) lack the flattened side and may be from the posterior part of the tooth row. The Bug Creek specimens appear to be unworn, and are unserrated; Lance Formation and Judith River Formation specimens may be either serrated or unserrated.

Theropoda? *incertae sedis*

A few teeth (MCZ 3680) of the straight-sided type figured by Estes (1964, fig. 69b) occur in the Bug Creek material.

INFRAORDER DEINONYCHOSAURIA ?
Family Dromaeosauridae ?

These short-crowned, sharply recurved teeth have about 40 serrations per 5 mm anteriorly, 30 posteriorly. They are of the same tooth type as those described by Cope as *Laelaps,* from the Judith River Formation of Montana. The Bug Creek specimens (MCZ 3695, Pl. 1C) are the smallest teeth of this type that we have seen, although several Lance Formation specimens approach them in size.

Laelaps is often included in *Dryptosaurus,* and Lance Formation specimens of the *Laelaps* type were questionably referred to *Dryptosaurus* by Estes (1964). The recent revision of Colbert and Russell (1969) suggests that *Laelaps* might better be included with the dromaeosaurs. Generic reference of this type of teeth, however, is difficult; the teeth from Bug Creek Anthills do not fall within any of the ranges of tooth serration number outlined by Colbert and Russell (1969, pp. 39-40). Sloan (1969, pers. comm.) found *Gorgosaurus* in other Bug Creek localities (Bug Creek West, Harbicht Hill), but its teeth are larger than any of the above.

ORDER ORNITHISCHIA
SUBORDER ORNITHOPODA
Family Hypsilophodontidae
Thescelosaurus neglectus Gilmore, 1913

A few teeth (MCZ 3649) resemble teeth of this species (see Sternberg, 1940, p. 483, figs. 1-8).

Family Pachycephalosauridae ?

Several teeth (MCZ 3729) are obtuse, with little development of a cingulum (Pl. 1A), and may belong to this family.

Family Hadrosauridae
Anatosaurus sp.

These teeth (MCZ 3646) are relatively common (for dinosaur teeth) in the Bug Creek sample and, in general, are somewhat smaller than most specimens from the Lance Formation. Most of the specimens appear to be heavily-worn teeth shed in replacement.

SUBORDER CERATOPSIA
Family Ceratopsidae
Triceratops sp.

As for *Anatosaurus*, the teeth referred here (MCZ 3647) are relatively common, smaller in general than most Lance Formation specimens, and are heavily worn, shed in replacement.

CONCLUSIONS

The striking feature of the lower vertebrate faunal list from Bug Creek Anthills (BCA) described here is its similarity to that from localities in the Lance Formation of Wyoming, especially University of California locality V5620 (Estes, 1964), as shown in Table 1. Mammals are excluded so that direct comparison of the lower vertebrates can be made. The taxonomic similarity is supplemented by a broad similarity of relative abundance of genera in the two localities; holosteans, salamanders, and lizards are the most common groups at both sites. Rather significant differences in the relative abundance of individual species occur, however, and may be ecological in origin; these differences will be discussed in more detail in Estes and Berberian (in press), and the mammalian

species included, but some general comments may be made now.

The diminished abundance, diversity and specimen size of the sharks at Bug Creek Anthills relative to those of V5620 probably indicates that BCA had reduced access to marine conditions. Turtles and lizards, also common at V5620, are again poorer in diversity, abundance, and preservation at BCA. Since the presumably more active, free-swimming salamanders and bony fishes are diverse, abundant, and well preserved at BCA, it is probable that a riparian habitat supporting the lizards and turtles was less accessible. The relative number of specimens and the specimen size of dinosaur material is less at BCA than at V5620; whether this condition is the result of depositional environment or is a reflection of the imminent extinction of the group is unknown, but the latter possibility is the more probable. Although further analysis may disprove this, we suggest that the vertebrate fossils at BCA were deposited in the larger, more open waterways of the floodplain, and that the site of deposition was farther from the adjacent shores, than it was at V5620. Sloan and Van Valen (1965) came to rather similar conclusions based on analysis of the mammalian fauna, and have expressed the faunal differences among the various Hell Creek Formation localities in terms of the proximal and distal community concept of Shotwell (1955).

Some mammals from Bug Creek Anthills are different from those of the Lance Formation localities and indicate a "Paleocene aspect," according to Sloan and Van Valen (1965). As noted above, the non-mammalian fauna of BCA differs little from that of the Lance. The additional taxa at BCA may be grouped into three categories: (1) Unique records, (2) Forms previously known only from the Paleogene, and (3) Records of taxa already known from both Cretaceous and Tertiary deposits but not occurring in the Lance Formation. The unique forms include the boid snake, the teiid lizard *Peneteius,* and the amphiumid salamander *Proamphiuma.* As these animals are representatives of living families and are related to modern genera, with the possible exception of the boid, it might be said that they are representative of an "advanced" element in the faunule. Since their stratigraphic ranges are unknown, however, this group does not specifically indicate a "Paleocene aspect." Only two taxa compose the second group. *Palaeolabrus,* a fish otherwise known only from a single Paleogene locality in Belgium, is a poor indicator of the Paleocene affinity of the BCA lower vertebrate fauna. One of the undescribed baenid turtles is known from middle Paleocene specimens from

Wyoming; this is its first Cretaceous record. Again, it is a rare form and a poor indicator of Paleocene relationships. The third group includes the fish *cf. Paralbula,* the frog *Scotiophryne,* and the turtle *Adocus.* These taxa are known from other Cretaceous and Paleocene deposits in North America, although they do not occur in the Lance Formation, and thus do not indicate "a Paleocene aspect" for the fauna. *Adocus,* apparently an advanced derivative of the late Cretaceous *Basilemys,* is most similar to specimens of *Adocus* from the Arapahoe Formation of Colorado, which, like the Hell Creek Formation, is of late Cretaceous age (Weimer, 1960, fig. 2).

We therefore conclude that the faunal differences between Bug Creek Anthills and V5620 localities indicate mainly minor ecological differences, and that there is little evidence for a significant difference in age or faunal type between the two sites. The geographic position of the Hell Creek localities, the unique character of the mammalian fauna, and the presence of lower vertebrates absent in the Lance Formation, probably indicate that, during late Cretaceous time, the Bug Creek Anthills fauna was more closely associated with a northern, perhaps climatically more temperate, aspect of the floodplain fauna of the Western Interior of North America.

Connections to a marine environment were less available at BCA than at V5620 as indicated by the reduced shark fauna. Since the Bearpaw Sea was regressing southeastward at latest Cretaceous time (Weimer, 1960), it may have been closer to V5620 than to BCA. It is also possible that the difference in access to marine conditions was only the result of local conditions, and that geographically, the actual sea was approximately equidistant from both localities; no evidence as to the actual geographic position of the strandline is available for latest Cretaceous time, however.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge our gratitude to Robert Sloan, whose enthusiastic support of our efforts and generous contribution of fossil material to many museums and universities has made this study possible. In addition to the MCZ collection listed and described in the body of this paper, we have had access to other collections, material from which has proved useful in assessment of variation although no additional taxa were present in them. These included unnumbered specimens from the University of Minnesota and the Saint Paul Science Museum, and catalogued

material as follows: Princeton University nos. 20468, 20554-20569, 20571-20573, 20806-20807; University of Kansas nos. 12453-12477; American Museum of Natural History nos. 8123-8129, 8131, 8140-8157, 9321-9329. Thomas Rich kindly sent a small collection from the University of California (Berkeley) as well as his personal collection.

Welcome discussion and help on various matters have come from Colin Patterson on *Lonchidion,* Cécile Poplin on amiids, Max Hecht on frogs, Allen Greer on scincid lizards, C. Wilson Kerfoot on *Cuttysarkus,* Mary Mickevich on dental histology of fishes, Dale Russell on dinosaur teeth, and Eugene Gaffney on baenid turtles. We are grateful to Donald Baird and Robert Sloan for helpful comments on the manuscript.

Figures 1-4 are by László Meszoly; the photographs are by Fred Maynard. This research was supported in part by National Science Foundation grants GB-1683, GB-4303, and GB-7176 to the senior author.

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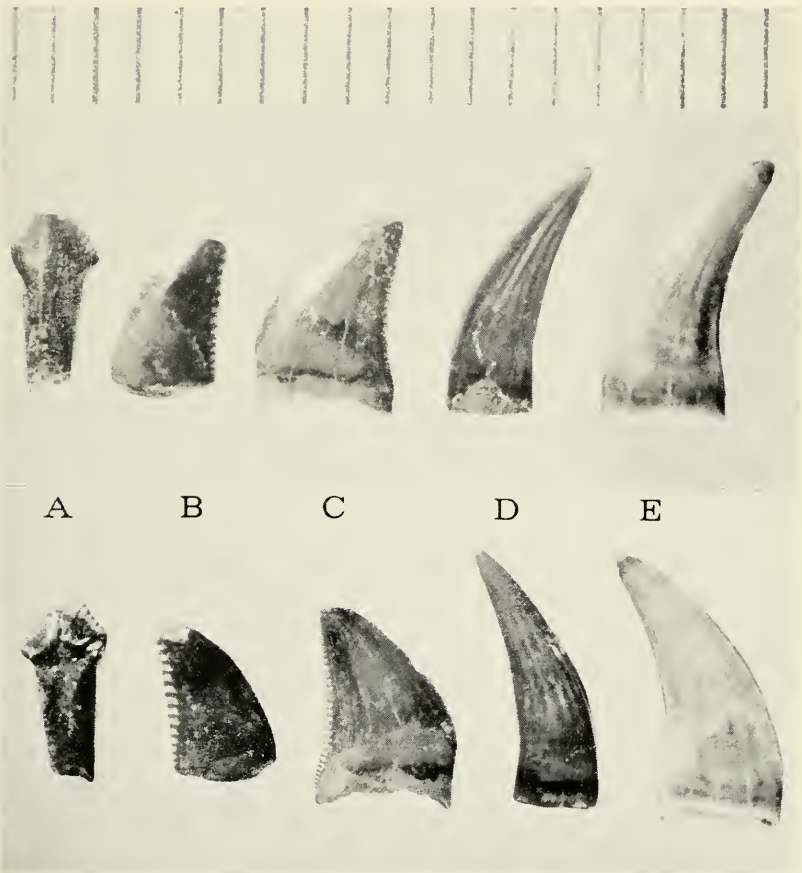

PLATE 1. Dinosaur teeth. A, ?Pachycephalosauridae, MCZ 3729; B, ?Coeluridae, MCZ 3694; C, ?Dromaeosauridae, MCZ 3695; D, *Paronychodon lacustris,* MCZ 3645; E, *cf. Paronychodon lacustris,* MCZ 3645; Bug Creek Anthills, Hell Creek Formation, McCone County, Montana; scale in mm.

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CAMBRIDGE, MASS. 30 DECEMBER, 1969 NUMBER 338

A NEW FROG OF THE GENUS *DISCODELES* (RANIDAE) FROM GUADALCANAL ISLAND

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and

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ABSTRACT. A fourth species of Solomon Island's *Discodeles*, *D. malukuna* (Ranidae), is described from 28 specimens collected near Malukuna, Guadalcanal, Solomon Islands. Among the species collected are three (*Hyla lutea*, a new species of *Batrachylodes*, and *Platymantis myersi*) previously unknown from Guadalcanal.

INTRODUCTION

Boulenger (1918a, 1920), in his treatment of the probable evolutionary lines within the large genus *Rana*, noted that the hylaranid and discodelid subgenera shared one characteristic, horizontal groove associated with the dilated disks at the tips of the toes and sometimes the fingers, but differed in the characteristics, structure of the omosternum, and degree of union of the outer metatarsals. He also (1918b) pointed out the close affinities of the genera *Cornufer* and *Platymantis* (both are currently included in one genus, *Cornufer*, by many authors) with *Discodeles*, particularly in the presence of a horizontal groove on the toe disks and in the union of the outer metatarsals throughout most or all of their length. Noble (1931, p. 521 ff), recognizing the subfamily Cornuferinae in the Ranidae, was obligated to raise *Discodeles* and *Hylarana* to generic rank, since *Rana (sensu stricto)* was retained in the subfamily Raninae. He noted the close relationships of the genera *Ceratobatrachus, Discodeles, Cornufer* and *Platymantis* in

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terms of the structural features discussed above and their geographical unity. He also called attention to the presence of a distinct, fleshy, median papilla on the tongue in *Discodeles* and its absence in *Cornufer*, a character somewhat difficult to use in many preserved specimens. Noble further surmised that direct development was characteristic of the species in this group of genera. This suggestion was based on knowledge of direct development of *Discodeles opisthodon* and *Cornufer guentheri* (op. cit., p. 64). This has been substantiated since for a number of species of *Platymantis* (includes *Cornufer*), see Alcala, 1962.

Prior to 1968, dating from the time of the descriptions of the three species of *Discodeles* (Boulenger, 1884), collections in the archipelago failed to reveal any further species. These explorations, however, did indicate that the three species were rather widely dispersed within the Solomons (Table 1). Therefore the discovery in 1968 by one of us (Webster) of a population in the mountains of Guadalcanal which represents a very distinct species was somewhat of a surprise.

The populations which have been found in New Britain and the Admiralty Islands are seemingly closely related to one or the other of the three species originally recognized. *Rana ventricosa* Vogt, 1912, (= *vogti*, Hediger, 1934) is very similar to and may be conspecific with *D. opisthodon* (Brown, 1952, pp. 36-37; Zweifel, 1960, pp. 4-7); and *Rana bufoniformis cognata* Hediger (1934) is synonomized with *D. guppyi* (Zweifel, 1960, p. 4).

Discodeles malukuna sp. nov.

Holotype. MCZ 79462, a mature male, collected at Malukuna area, elevation about 2500 feet, Guadalcanal Island, July 2, 1968, by T. Preston Webster.

Paratypes. MCZ 79463-79489, from the same area as the holotype.

Diagnosis. A relatively small *Discodeles*, at least for a sample of males as compared to other known species, largest available male measuring 58.3 mm in snout-vent length; head broad relative to snout-vent length (Fig. 2); eye relatively large, slightly less than, to about equal to, length of snout; first finger longer than second or fourth when adpressed; tips of fingers not dilated, rounded, lacking a terminal circummarginal groove; first and fifth toe about one-fourth webbed, web reaching the distal edge of the tubercle of the inner toe and failing to reach or barely reaching the distal tubercle

TABLE 1

Distribution of the species of *Discodeles* in the Solomon Islands.

Species	Bougainville Group							New Georgia Group						Guadalcanal Group				San Cristobal Group		
	Buka	Bougainville	Fauro (Faro)	Shortland (Alu)	Mono (Treasury)	Choiseul	Isabel (Santa Ysabel)	Vella Lavella	Ronongo (Ganongga)	Kolombangara (Kulumbangara)	New Georgia	Rendova (Hammond)	Gatukai	Guadalcanal	Florida (Nggela)	Tulagi	Malaita	San Cristobal	Ugi	Santa Ana
Discodeles malukuna														x						
Discodeles bufoniformis		x	x	x	x	x	x	x	x	x	x					x	x		x	
Discodeles guppyi		x	x	x			x				x	x	x	x	x		x			
Discodeles opisthodon		x	x	x	x					x								x	x	x

of the outer toe; second and third toes about one-half webbed; outer metatarsals not firmly united in the distal fourth, or less, of their length; venter grayish brown to blackish, usually with numerous white spots.

Description. A relatively small *Discodeles* as compared to known species; the snout-vent length, about 43 to 58 mm for 11 males, is unknown for adult females (the largest female, measuring 63.2 mm in snout-vent length, is possibly almost mature as judged by the fact that the oviducts are just beginning to show shallow convolutions); habitus tapering from the head to the groin; head breadth 115 to 123 per cent of head length for 11 mature males, 89 to 99 per cent of tibia length, and 44 to 49 per cent of snout-vent length for the same group of males; diameter of eye 91 to 102 per cent of length of snout; diamenter of tympanum 39 to 55 per cent of diameter of eye; interorbital distance 17 to 21 percent of the head length for 11 mature males; upper jaw round, pointed, protruding; loreals moderately oblique and concave; fingers without webs; first finger longer than the second or fourth when adpressed; tips of fingers bluntly rounded, undilated (Fig. 4), without a circummarginal groove; subarticular tubercles large, prominent but not pointed; a few large, faint, palmar tubercles; metatarsal tubercles low, rounded, outer broadly oval, inner more elongate; toes with moderate webs, strongest between second—third and third—fourth; web reaching the distal edge of the subarticular tubercle of the inner toe and not or barely reaching the distal tubercle of the outer toe (Fig. 5); tips of toes rounded, moderately dilated and depressed, the ventral part of the disk separated from

the dorsal by a circummarginal groove; subarticular tubercles large and prominent but not sharply protruding; outer metatarsal tubercles small and round, inner moderately narrow and long (Fig. 5); skin of dorsum, lateral surfaces, and upper surfaces of the limbs smooth except for a pair of folds between the postorbital and axillary region; large, flat tubercles on posterior and ventral surface of thighs; venter faintly granular posteriorly in some instances.

Color (in preservative). Grayish brown to blackish brown on the dorsum; lateral surfaces and limbs lighter grayish to grayish brown; upper loreal region, borders of eyelids, upper tympanum and edges of urn-shaped folds (especially at posterior ends) black; lips with two prominent dark bars; a black anal patch and hind limbs marked by narrow, dark transverse bands; venter grayish to blackish brown with numerous light spots.

Measurements of holotype (in mm). Snout-vent length 58.3; length of head to posterior edge of tympanum 22.3; breadth of head 25.9; diameter of eye 7.7; diameter of tympanum 3.7; length of snout 8.2; interorbital distance 4.0; length of hind limb 92.0; length of tibia 28.5; length of third finger to proximal edge of basal tubercle 7.9; length of first finger to base of tubercle 5.6.

Etymology. The species name is that of the type locality in the central mountains of Guadalcanal.

Remarks. Of the four known species of the genus *Discodeles,* all present in the Solomon Islands, this is the most readily distinguished because of the extremely reduced webbing between the toes, the lack of warty tubercles on the dorsum and upper surfaces of the hind limbs (these are present in some degree even in *D. guppyi,* the least tuberculate of the other three species), the urn-shaped pattern formed by the pair of folds on the anterior part of the dorsum, and the conspicuous black markings.

The intuitive evaluation, head broader than for other known species of the genus (particularly for larger, mature specimens), is borne out by plotting head breadth against snout-vent length (Fig. 2), although this ratio is only slightly greater than for *bufoniformis.* Moreover, differential growth patterns for the four species are evident in several proportions: (1) head breadth relative to tibia length, Figure 3; (2) interorbital distance relative to head length, Figure 1.

In such characters as the lack of dorsal tubercles, the reduced webbing of the toes (intermediate between that of *Platymantis guppyi* and *Discodeles opisthodon*), and the anterior, urn-shaped folds, *D. malukuna* is somewhat intermediate between the other

species of *Discodeles* and those species of *Platymantis* exhibiting the greatest degree of webbing between the toes. This appears to further substantiate the probable close relationship between *Discodeles* and *Platymantis* postulated by Noble (1931, p. 523).

Previously seven species of amphibians were known from Guadalcanal (Brown, 1952). These included:

Hyla thesaurensis
Batrachylodes vertebralis
Ceratobatrachus guentheri
Discodeles guppyi
Platymantis guentheri
Platymantis papuensis weberi
Rana papua novaebritanniae

In addition to *Discodeles malukuna,* Webster's collection from the mountainous area around Malukuna includes specimens of three other previously unrecorded species: *Hyla lutea, Batrachylodes* new species,[1] and *Platymantis myersi.*

ACKNOWLEDGMENTS

Thanks are due to Mr. G. F. C. Dennis and his son Tony and to the people of Malkuna. Partial support in the field was provided by NSF grant GY 4555 to T. P. Webster and by NSF 6944 to Ernest E. Williams. Illustrations were prepared by Walter Zawojski, Stanford University.

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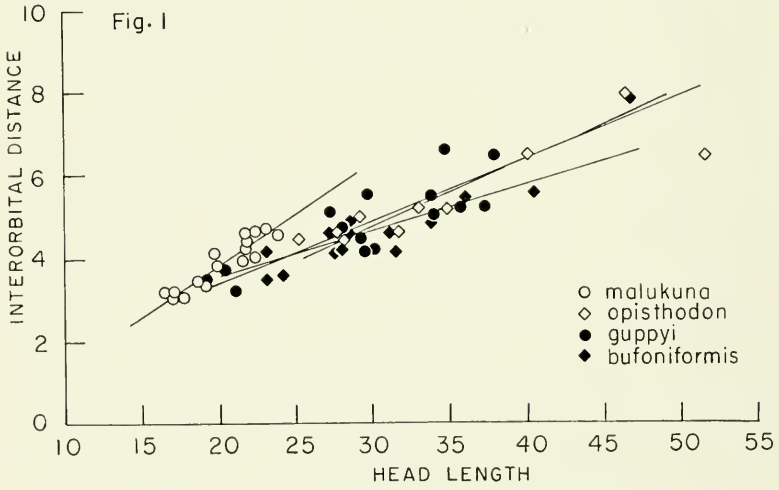

Fig. 1. Differences in interorbital distance relative to head leng.h for four species of *Discodeles*. (Measurements in mm.)

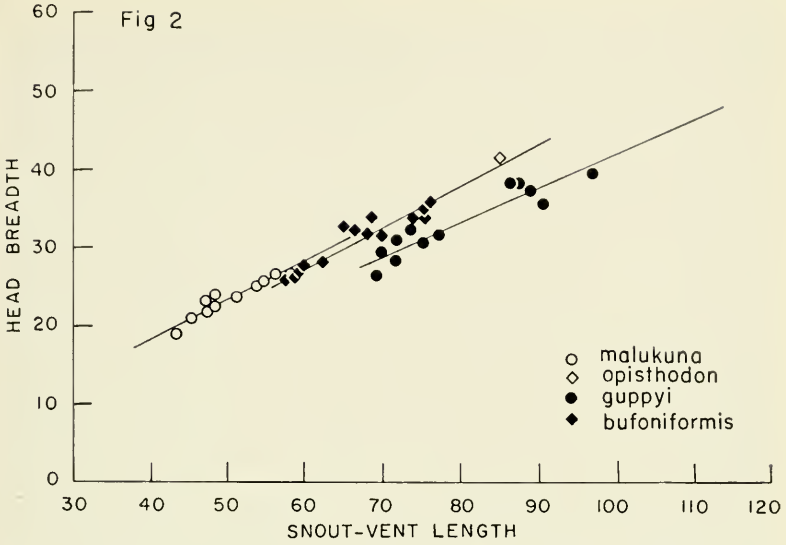

FIG. 2. Differences in head breadth relative to snout-vent length for four species of *Discodeles*. (Measurements in mm.)

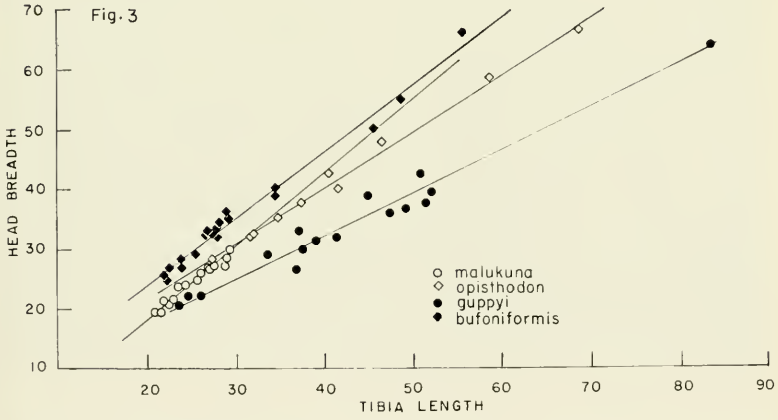

FIG. 3. Differences in head breadth relative to tibia length for four species of *Discodeles*. (Measurements in mm.)

FIG. 4. *Discodeles malukuna*: inferior view of hand.

FIG. 5. *Discodeles malukuna*: inferior view of foot.

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CAMBRIDGE, MASS. 30 DECEMBER, 1969 NUMBER 339

THE GENUS *STENOONOPS* (ARANEAE, OONOPIDAE) IN PANAMA AND THE WEST INDIES

Arthur M. Chickering

ABSTRACT. A total of seventeen species of the genus *Stenoonops* are recognized in this paper. Eleven species are described as new. Six of these are described from Jamaica, W. I., two from Puerto Rico, two from St. Thomas, U. S. Virgin Islands, and one from Antigua, B. W. I. *Scaphioides reducta* Bryant, 1942 from St. Croix, U. S. V. I., is placed in *Stenoonops*.

This is the fifth paper in the series planned for publication on the various genera in the Family Oonopidae in Central America and the West Indies.

Once more I take this opportunity to express my appreciation for the continued aid and encouragement extended to me by the staff of the Museum of Comparative Zoology, Harvard University. Grants GB-1801 and GB-5013 from the National Science Foundation have made it possible for me to carry on extensive collecting activities in Panama, Costa Rica, Florida, and the West Indies during the years 1963-1968 and to continue my studies in the Museum of Comparative Zoology during that period. My acknowledgements are gratefully extended to the following persons for the loan of types and other specimens to aid me in more completely understanding the genus under consideration: Dr. J. G. Sheals and Mr. D. J. Clark of the Department of Zoology, British Museum (Natural History); Dr. Willis J. Gertsch, recently retired from the American Museum of Natural History, New York City, and also Mr. Wilton Ivie, Research Fellow in the American Museum of Natural History.

The types of *Stenoonops phonetus* sp. nov. will be deposited in the American Museum of Natural History. All other types described in this paper together with my entire collection of the genus *Stenoonops* will be deposited in the Museum of Comparative Zoology, Harvard University.

Genus STENOONOPS Simon, 1891

The type species is *Stenoonops scabriculus* Simon by monotypy, based upon a male from St. Vincent, B. W. I., which I have had on loan for study. Since the recognition of the genus in 1891, only three additional new species have been recognized and assigned to this genus in the region at present under study. One additional species from St. Croix, U. S. Virgin Islands, was recognized as new by Miss Bryant and assigned to a new genus but is now included in *Stenoonops*. One species has been known only from females; one species has been known from both sexes; all others have been known only from males.

In addition to the general family characteristics, the features of the genus *Stenoonops* as observed in this study may be stated as follows: total length varies from about 1.1 mm to 2.1 mm. The general shape and height of the carapace differs considerably in the various species included in this paper. The ventral margin of the carapace is often plainly serrated. The eyes are six in number, arranged in two rows in a fairly compact group; the ALE are nearly always at least slightly the largest of the six and the distance between them varies considerably; the posterior row is typically somewhat recurved but occasionally is straight or gently procurved. The chelicerae, maxillae and lip usually appear to be without conspicuous modifications; a notable exception is furnished by *S. insolitus* sp. nov. The legs are moderately long and slender without great differences in length, without true spines but with many hairs and bristles. Trichobothria are present but their exact placement and specific differences among species have not been accurately determined. The male palp is simple and without special modifications except in the case of the tarsus, which exhibits a high degree of variation among the recognized species under study at the present time. In species like *S. portoricensis* and *S. insolitus* sp. nov., the distal palpal tarsal features are conspicuously characteristic, but in numerous other species, these structures are so obscure and so difficult to differentiate that errors are always confronting the investigator. Jets of semen extending from the distal end of the tarsal bulb are often quite conspicuous, sometimes deceptive and, perhaps, lead to erroneous conclusions regarding the extent and shape of the embolus. I think I have more difficulties in making decisions at this point than in any other genus thus far studied in the family Oonopidae. The abdomen is completely lacking a dorsal scutum but scuta are more or less well defined at the anterior end of the venter. Typically, there is a fairly well-defined epigastric

scutum reaching forward to meet the pedicel and a narrow ventral scutum, often overlooked in descriptions, just behind the genital groove. I think I have usually been able to discern these scuta even when they lack the usual yellowish or brownish coloration. The epigynal areas in females are also often very difficult to discern and to represent in drawings. In these cases reliance has been placed upon characteristics of the eyes, features of the carapace, sternum, etc. The spinnerets appear to be without special modifications; no chitinous sclerite has been observed at the base of the spinnerets as is so often observed in other genera in the family. A pair of dark-colored subsurface structures typically appear on the venter shortly anterior to the bases of the anterior spinnerets, but they are lacking in some species.

Although uncertainties still persist to trouble the author of this paper, it seems at this time that I must recognize a total of seventeen species of the genus *Stenoonops* from the region under consideration. This list may be given as follows: *Stenoonops cletus* sp. nov.; *Stenoonops dimotus* sp. nov.; *Stenoonops econotus* sp. nov.; *Stenoonops halatus* sp. nov.; *Stenoonops hoffi* sp. nov.; *Stenoonops insolitus* sp. nov.; *Stenoonops lucradus* sp. nov.; *Stenoonops macabus* sp. nov.; *Stenoonops minutus* Chamberlin and Ivie; *Stenoonops nitens* Bryant; *Stenoonops noctucus* sp. nov.; *Stenoonops padiscus* sp. nov.; *Stenoonops petrunkevitchi* Chickering; *Stenoonops phonetus* sp. nov.; *Stenoonops portoricensis* Petrunkevitch; *Stenoonops reductus* (Bryant); *Stenoonops scabriculus* Simon. Only one species is known from each of the following: Panama; St. Vincent, B. W. I.; and Antigua, B. W. I. Three species are known from Puerto Rico and six are known from Jamaica, W. I. Two species are known from St. Croix, U. S. V. I.; three are known from St. Thomas, U. S. V. I.; and four have been identified from St. John, U. S. V. I. Three males and two females from Virgin Gorda, British Virgin Islands, are at present assigned to *S. nitens* Bryant with some uncertainty. A single female from St. Lucia, B. W. I., is also, with some uncertainty, assigned to *S. nitens* Bryant. One species has been recorded from both North and South Bimini, Bahama Islands. Either because of ocular anomalies or the obscurity of features necessary for definite identification, a few specimens from the region under study have been left unassigned to any species.

STENOONOPS CLETUS sp. nov.

Figures 1-6

Holotype. The male holotype is from Jamaica, W. I., St. Catherine Parish, three miles east of May Pen, November 22, 1957.

The name of the species is an arbitrary combination of letters.

Description. Total length 1.28 mm, exclusive of the slightly extended spinnerets. Carapace 0.6 mm long; 0.46 mm wide opposite posterior border of second coxae where it is widest; 0.3 mm tall; rises somewhat just posterior to PME and then gently arches along midline to beginning of posterior declivity with tallest point shortly before the beginning of the declivity (Fig. 1 of paratype); with no median thoracic groove or pit; surface finely granular; sparsely covered by short, dark hair; ventral margin very finely serrated. Eyes: six in two rows as usual; in a compact group (Fig. 2); viewed from above, posterior row definitely recurved and occupies about three-fourths of width of carapace at that level. Ratio of eyes ALE : PME : PLE=7 : 6 : 6. All eyes somewhat irregular in outline; long diameters always used for measurements. ALE separated from one another by about one-seventh of their diameter; separated from PME by about one-eighth of their diameter and from PLE by about one-third of the diameter of the latter. PME contiguous for nearly one-third of their circumference; tangent to PLE. Posterior row wider than anterior row in ratio of about 17 : 12. Only a moderate amount of black pigment in ocular region. Height of clypeus equal to about two-thirds of the diameter of ALE; clypeus somewhat convex and provided with six stiff bristles, two of these very long, others short. Chelicerae: vertical; essentially parallel; tapering gradually from base to tip; about 0.11 mm long; fang regularly curved and slender; no teeth observed along fang groove in dissected specimen; apparently without basal boss. Maxillae and lip essentially typical of the genus. Sternum: somewhat convex; finely granular; only moderately lobed and grooved; only a little longer than wide between second and third coxae; posterior end apparently somewhat bilobed and just opposite bases of fourth coxae which are separated by nearly 1.2 times their width. Legs: 4123 in order of length; true spines lacking but some bristles are spiniform. Palp: short; simple except for the tarsus which is normally inflated and inconspicuously terminated (Figs. 3-4); right palpal tarsus with a conspicuous jet of semen extended from embolus. Abdomen: ovoid; widest in the middle; 0.43 mm tall; quite typical of the genus in general; epigastric and ventral scuta fairly well outlined but division between the two very obscure; the pair of subsurface structures just anterior to spinnerets only dimly outlined. Color in alcohol: carapace a clear yellowish brown; sternum somewhat lighter; legs yellowish with some variations; abdomen yellowish white with some iridescence; scuta somewhat darker yellowish.

Female paratype. Total length 1.54 mm. Carapace 0.56 mm long; 0.44 mm wide; 0.26 mm tall; otherwise essentially as in male (Fig. 5). Eyes: in nearly all essential features, these seem to be in agreement with those of the male; ALE are somewhat further apart than in the male. Chelicerae, maxillae, lip, and sternum all nearly as described for the male holotype. Legs: 4123 in order of length as in male; palp probably without a claw; trichobothria observed but exact placement not determined. Abdomen: 1.04 mm long; regularly ovoid in shape; scuta and epigynal area essentially as shown in Figure 6.

Diagnosis. This species seems to be closely related to *Stenoonops nitens* Bryant. It differs from that species chiefly in the features of the male palp, the sternum, and the shape of the carapace.

Records. The described female paratype was taken with the male holotype. Male and female paratypes are in my collection from several localities in the following named parishes in Jamaica, W. I.: Trelawney; St. Andrew; St. Thomas; and St. Catherine.

Stenoonops econotus sp. nov.

Figures 7-9

Holotype. The female holotype is from Puerto Rico, Mayagüez, University farm north of University campus, January 31, 1964. The name of the species is an arbitrary combination of letters.

Description. Total length 1.47 mm exclusive of the somewhat extended spinnerets; including these organs total length is 1.54 mm. Carapace 0.56 mm long; 0.4 mm wide opposite posterior borders of second coxae where it is widest; about 0.2 mm tall (Figs. 7-8); plainly serrated along ventral margins; gently arched along midline from PME to beginning of steep posterior declivity opposite third coxae; unevenly granular along lateral and posterior surfaces; no median thoracic groove or pit present. Eyes: six as usual in a compact group; occupy five-sixths of width of carapace at that level; posterior row gently recurved, viewed from above and wider than anterior row in ratio of about 16 : 13. Ratio of eyes ALE : PME : PLE = nearly 6 : 5 : 5. ALE separated from one another only by a broad line; separated from PME and PLE by nearly the same distance. PME contiguous to one another and barely separated from PLE. Height of clypeus equal to width of somewhat oval ALE. Chelicerae, maxillae, and lip apparently typical of females of the genus. Sternum: longer than wide in ratio of about 4 : 3; widest just behind second coxae at level of a lateral lobe; lobes and grooves well developed; posterior end

pointed and extended just opposite bases of fourth coxae which are separated by nearly 1.3 times their width. Legs: 4123 in order of length; otherwise as usual in the genus. Abdomen: ovoid and quite typical of the genus in general; the typical dark, ventral, subsurface spots barely visible just anterior to spinnerets; epigastric and ventral scuta well outlined but occupy only about half the width of the venter at that level (Fig. 9); epigynal area obscurely distinctive. Color in alcohol: carapace a dark brown with irregular, darker, radiating, lateral and posterior streaks caused by concentrations of granulations; only a moderate amount of black pigment in ocular area; sternum a lighter yellowish brown; legs and mouth parts yellowish with variations; abdomen yellowish on dorsum with an irregular white, transverse band about two-thirds from base and a pair of white areas at anterior end; venter generally yellowish with scuta a light yellowish brown.

Diagnosis. This species appears to be somewhat closely related *to Stenoonops nitens* Bryant, but it differs from that species in respect to color pattern, scuta, and relative position of eyes.

Record. The male is unknown and there are no paratypes.

Stenoonops nitens Bryant

Figures 10-13

Stenoonops nitens Bryant, 1942: 321, figs. 5, 10. The holotype male from St. Croix, U. S. Virgin Islands, is in the Museum of Comparative Zoology, Harvard University, examined.

Numerous specimens of this species have been collected on St. Croix, and a male and a female have been selected for study; a brief report follows:

Male. Total length exclusive of the extended spinnerets and chelicerae 1.14 mm; including these structures total length is 1.26 mm. Carapace 0.53 mm long; 0.4 mm wide; nearly 0.18 mm tall (Fig. 10). Ratio of eyes ALE : PME : PLE = nearly 5 : 4.5 : 4. ALE separated from one another by nearly one-fourth of their diameter (Fig. 11). The clypeus is quite porrect and with height about equal to diameter of ALE. The scuta are fairly well outlined and closely similar to those of female but are less well delineated. The male palp is very obscure. The holotype was described as having "two very slender points at tip." I believe that these "points" are simply the lateral boundaries of the embolus, which extends as a very short tube that varies in appearance in different individuals and in different positions in the same individual (Fig. 12).

Female. Total length exclusive of the spinnerets and chelicerae 1.21 mm; including these structures total length is about 1.29 mm. Carapace nearly the same as in male. Figure 13 represents the abdominal scuta and epigynal area of the female.

The specimens now assigned to this species include a group regarded for a considerable length of time as another new species. At present they are regarded as what might be considered a variety by some taxonomists. My collection now contains many specimens of both sexes from the following localities: St. Croix, U. S. Virgin Islands, vicinity of Frederiksted, March, 1964 and September, 1966; several localities on St. Thomas, U. S. Virgin Islands, February, 1964 and July-August, 1966; St. John, U. S. Virgin Islands, March 1964 and September, 1966. Two females collected near Mayagüez, Puerto Rico, January, 1964, may possibly belong to this species. This suggests the probability that careful collecting in the West Indies will greatly extend the known territorial range of this species. A female collected in Costa Rica on Mt. Irazu on July 27, 1965, has been regarded as a possible member of this species but is now left unplaced.

STENOONOPS PORTORICENSIS Petrunkevitch

Figures 14-18

Stenoonops portoricensis Petrunkevitch, 1929: 72, figs. 61-63. The holotype male from Toa Alta, Puerto Rico, W. I., is in the American Museum of Natural History, New York City, examined. Roewer, 1942: 280; Bonnet, 1958: 4156.

I did not collect the male of this species during my period of field work in Puerto Rico in 1964. The male holotype is the only male specimen known at present and, unfortunately, it is in poor condition for study. The right palp, figured by Dr. Petrunkevitch, is missing, and I have found it impossible to see the parts in the left palp as originally described. More careful collecting is needed to add to our knowledge of the genus in this island. The female described here was for a time regarded as representing a new species but, following observations on the holotype and awaiting more complete knowledge regarding the species, I have decided to treat it as a female of *Stenoonops portoricensis.*

Female. Total length 1.63 mm, including the extended spinnerets; excluding the spinnerets, the total length is about 1.5 mm. Carapace 0.6 mm long; about 0.5 mm wide opposite second coxae where it is widest; about 0.31 mm tall; considerably raised behind

PME and then nearly level to beginning of steep posterior declivity; regularly rounded along ventral margin; closely similar to carapace of male holotype (Figs. 14, 18). Eyes: essentially as indicated for male in original description of holotype; ratio of eyes ALE : PME : PLE = nearly 6 : 6 : 5 (Fig. 15). Clypeus obscured by tuft of bristles. Mouth parts and legs appear essentially as described for the holotype male except for the palps; these parts with many short hairs but no true spines. Sternum: with many short, black hairs obscuring faintly indicated lobulations. Abdomen also with many short, black hairs as described for the male (Fig. 16); with a weakly outlined epigastric scutum occupying less than half the width of the venter and a very narrow ventral scutum; epigynal area very indistinct (Fig. 17).

Records. The described female is from the University farm north of the University campus, Mayagüez, Puerto Rico, January 25, 1964. Two females collected in the vicinity of Mayagüez have not yet been placed satisfactorily in any known species. Several specimens in the collection of the Museum of Comparative Zoology, tentatively assigned to this species, have been reassigned to other genera or left unplaced because of uncertainties.

Stenoonops dimotus sp. nov.

Figures 19-20

Holotype. The female holotype is from Jamaica, W. I., St. Andrew, Ferry, near Red Hills Road, October 28, 1957. The name of the species is an arbitrary combination of letters.

Description. Total length 2.09 mm, exclusive of the somewhat extended chelicerae; including these structures, total length is 2.14 mm. Carapace about 0.81 mm long; 0.57 mm wide opposite posterior border of second coxae where it is widest; 0.29 mm tall; ventral margin finely serrated; otherwise essentially typical of females of the genus (Fig. 19). Eyes: six in a compact group; outlines obscure and irregular. Viewed from above, posterior row definitely recurved and longer than anterior row in ratio of about 17 : 13; ALE conspicuously silvery, PME less so; posterior row occupies about three-fourths of width of carapace at that level; PME apparently tilted outward so that outlines are very unusual in appearance (Fig. 20). Ratio of eyes ALE : PME : PLE = nearly 6 : 5 : 5. ALE separated from one another by about their radius. and from PME and PLE by slightly more than half their radius. PME contiguous to one another and narrowly separated from PLE. Only a small amount of black pigment in ocular area; area usually

black is here reddish brown. Height of clypeus equal to slightly more than the diameter of ALE; clypeus with several stiff, black bristles and quite porrect. Chelicerae, maxillae, and lip apparently quite typical of females of the genus. Sternum: plainly lobed in fairly typical manner; longer than wide in ratio of nearly 4 : 3; widest just behind second coxae where a lobe extends laterally; with numerous incurved bristles; posterior end pointed and not quite reaching proximal end of fourth coxae, which are separated by nearly their width. Legs: 4123 in order of length; only slight difference in lengths of fourth and first legs; many hairs, bristles and several trichobothria observed but no true spines. Abdomen: typical in general of females of the genus; scuta very obscure with outlines difficult to follow; ventral scutum hardly more than a transverse line; obscurity of epigynal area prevents any clear understanding of the characters of this region. Color in alcohol: carapace light yellowish brown, darkened somewhat along lateral sides and margins; with almost no black pigment in ocular region; sternum nearly like carapace; first two pairs of legs only a little lighter than carapace; third and fourth legs somewhat more yellowish; abdomen nearly clear white throughout with many short, dark hairs.

Diagnosis. This species appears to be closely related to *Stenoonops portoricensis* Petrunkevitch and, apparently, belongs to the group containing *Stenoonops macabus* sp. nov. and several other species. The eyes appear to be unique, however, and the ventral scutum is unusually narrow.

Records. The male is unknown and there are no paratypes.

Stenoonops insolitus sp. nov.

Figures 21-26

Holotype. The male holotype is from Jamaica, W. I., St. Catherine Parish, three miles east of Old Harbour, October 21, 1957. The name of the species is a Latin adjective meaning unusual, chosen because of the unusual anatomical features.

Description. Total length 1.56 mm. Carapace 0.68 mm long; 0.48 mm wide opposite second coxae where it is widest; 0.26 mm tall; rises slightly behind PME and then is nearly level along midline to beginning of posterior declivity where there are rough granulations; surface in general finely granular, ventral margin very finely serrated but visible only when viewed from above; otherwise essentially typical of the genus (Fig. 21). Eyes: six as usual in the genus. Ratio of eyes ALE : PME : PLE = nearly 6.5 : 5.5 : 5.

Posterior row gently recurved; occupies about two-thirds of width of carapace at that level; outlines of eyes somewhat obscure. ALE separated from one another by nearly one-third of their diameter (Fig. 22); nearly contiguous to PLE and separated from PME by a broad line; PME contiguous for about one-third of their circumference and barely separated from PLE. Height of clypeus nearly equal to two-thirds of the diameter of ALE. Chelicerae and lip essentially typical of the genus. Maxillae: general form shown in Figure 23; distal end of each provided with a pair of very long and conspicuous spines not seen in any other species known to me. Sternum: longer than wide in ratio of about 3 : 2; not extended between fourth coxae, which are separated by somewhat more than their width; with marginal lobes and grooves moderately well developed; third coxae subglobose, others more elongated. Legs: 4123 in order of length; no true spines observed but spiniform bristles are numerous; trichobothria observed on tibiae and metatarsi. Palp: essential features shown in Figures 24-26. Distal end of tarsus appears divided; minor differences in the form of the distal end of the palpal tarsi have been noted among the paratypes. Abdomen: ovoid; typical of the genus in general; surface with numerous short, dark hairs; the usual scuta are present but barely visible. Color in alcohol: carapace and sternum a clear yellowish brown; legs and mouth parts somewhat lighter; abdomen almost white.

Female paratype. Total length 2.07 mm. Carapace 0.77 mm long; 0.55 mm wide opposite second coxae where it is widest; about 0.28 mm tall; otherwise essentially as in male. Eyes: ratio of eyes almost exactly as in male. Spiniform bristles on clypeus conspicuous. Posterior row of eyes occupies about two-thirds of width of carapace at that level; otherwise essentially as in male. Chelicerae, maxillae, and lip as usual in females of the genus; there are no indications of the conspicuous maxillary spines possessed by the male. Sternum: features somewhat more conspicuous than in male; slightly more than two-thirds as wide as long; bristles conspicuous on lobes and between bases of fourth coxae, which are separated by somewhat more than their width; grooves between marginal lobes quite conspicuous. Legs: 4123 in order of length; essentially as in male holotype. Abdomen: essentially as in male except for the scuta and epigynal area, which are also very poorly outlined. Color in alcohol: essentially as in male; the paired dark spots on the venter just anterior to the first pair of spinnerets, so frequently seen in species of this genus, were not seen in the holotype male but are present here as three pairs of faintly outlined

dots somewhat irregularly placed and are completely lacking in some paratypes.

Diagnosis. This species appears to belong to the group of species represented by *Stenoonops portoricensis* Petrunkevitch and *Stenoonops petrunkevitchi* Chickering, but the distinctive features of the male palp and, especially, the maxillary spines of the male definitely establish it as a new species.

Records. The described female paratype was taken with the holotype male. Two male paratypes were also taken with the holotype. Eight males and five females are also in the collection from Jamaica, W. I., as follows: St. Ann Parish near Moneague, May 20, 1956 (C. C. Hoff); St. Andrew Parish, Stony Hill, October 18, 1957; St. Catherine Parish, Guanaboa Vale, December 4, 1957; St. Catherine Parish, Evarton, November 29, 1957, and Ferry, June 19, 1954.

STENOONOPS LUCRADUS sp. nov.

Figures 27-28

Holotype. The male holotype is from St. Thomas, U. S. Virgin Islands, August 25, 1966, in the vicinity of Charlotte Amalie from hay and weed debris. The name of the species is an arbitrary combination of letters.

Description. Total length exclusive of the extended spinnerets 1.45 mm; including the spinnerets total length is about 1.55 mm. Carapace about 0.59 mm long (slightly overlapped by abdomen); nearly 0.45 mm wide opposite second coxae where it is widest; 0.24 mm tall; gently arched from PME along midline to a slightly raised portion just before beginning of steep posterior declivity; first half of declivity very steep, second half gradually descending; a tuft of hairs accentuates the top of the declivity. Eyes: six as usual in a compact group; very little difference in long axes of the three pairs of eyes but some differences in shape have been noted; posterior row slightly recurved (Fig. 27). ALE separated from one another by about two-fifths of their diameter; separated from PME by about three-tenths of their diameter and from PLE by one-fifth of their diameter. PME contiguous as usual and separated from PLE only by a line. With several bristles and a moderate amount of black pigment in ocular area. Clypeus with numerous bristles and with height about equal to the diameter of ALE. Chelicerae, maxillae, and lip obscure and difficult to observe but apparently typical of the genus and without special modifications.

Sternum: moderately convex; moderately lobed and only slightly grooved; with posterior end unusually lobed just before bases of fourth coxae, which are separated by about their width; margins with stiff, black, incurved bristles; first coxae somewhat elongated, others nearly subglobose. Legs: 4123 in order of length; no true spines observed; many hairs and bristles present. Palp: only tarsus inflated; with a very distinctive, twisted embolus (Fig. 28). Abdomen: typical of the genus; with scuta and genital area barely discernible. Color in alcohol: carapace a medium yellowish brown, lighter along median region and darker along lateral sides; with numerous black hairs; ocular region with a moderate amount of black pigment; sternum nearly the same as the carapace; legs somewhat lighter; abdomen nearly white with many short, black hairs; with no evidence of the dark spots on the venter just anterior to the spinnerets.

Female paratype. Total length 1.46 mm, exclusive of the extended spinnerets; including the spinnerets total length is 1.6 mm. Carapace about 0.61 mm long (slightly overlapped by abdomen); nearly 0.46 mm wide opposite second coxae where it is widest; about 0.28 mm tall; gently arched from just behind PME to beginning of posterior declivity nearly opposite third coxae; first half of declivity steep, lower half a very gradual descent to posterior border. Eyes: quite different in appearance from those of male; seen from above, posterior row very slightly procurved but almost straight; posterior row occupies about two-thirds of width of carapace at that level and is wider than anterior row in ratio of nearly 3 : 2. Ratio of eyes ALE : PME : PLE = nearly 5 : 5 : 4. PME tilted outward so they appear very narrow when viewed from above; their appearance is similar to that of the PME of *Stenoonops dimotus* sp. nov. from Jamaica. ALE separated from one another by a little less than their radius and separated from PME by nearly the same distance; separated from PLE by a little less than this distance. PME contiguous as usual and nearly contiguous to PLE at one point. Height of clypeus nearly equal to diameter of ALE. Chelicerae, maxillae, lip, and sternum essentially as in male. Legs: 4123 in order of length but with only small differences among them. Abdomen: almost exactly as in male with scuta hardly discernible; epigynal area without observable distinctive features. Color in alcohol: also almost exactly as in male holotype.

Diagnosis. This is another species that appears to be closely related to *Stenoonops petrunkevitchi* Chickering and *Stenoonops portoricensis* Petrunkevitch. The features of the palpal tarsus are quite distinctive and definitely serve to establish it as a new species.

Records. The described female is from St. John, U. S. Virgin Islands, July 23, 1966. One male was taken with the female.

STENOONOPS MACABUS sp. nov.
Figures 29-30

Holotype. The male holotype is from Jamaica, W. I., St. Catherine Parish, three miles east of May Pen, November 22, 1957. The name of the species is an arbitrary combination of letters.

Description. Total length 1.78 mm. Carapace 0.66 mm long; 0.5 mm wide opposite second coxae where it is widest; 0.22 mm tall; slightly raised just behind PME and then nearly level along midline to beginning of steep posterior declivity; with no median thoracic groove or pit; surface very finely granulate and corrugated; quite typical of the genus in general. Eyes: six in two rows as usual in the genus. Ratio of eyes ALE : PME : PLE = nearly 11 : 9 : 7 (outlines somewhat obscure). Posterior row occupies about two-thirds of width of carapace at that level and is moderately recurved, viewed from above (Fig. 29). ALE separated from one another by about their radius, from PME by about half their radius and from PLE by about one-fifth of their diameter. PME contiguous for about one-fourth of their circumference and nearly tangent at one point to PLE. Posterior row of eyes wider than anterior row in ratio of about 6 : 5. The clypeus bears a row of long, stiff bristles; height of clypeus nearly equal to three-fourths of long axis of ALE. Chelicerae as usual in the genus. Maxillae long, slender, slightly convergent. Lip essentially typical of the genus; reaches nearly to middle of maxillae. Sternum: essentially typical of the genus; with lobes and grooves along margins moderately well developed; bluntly terminated shortly before bases of fourth coxae which are separated by a little less than their width. Legs: 4123 in order of length; spines are lacking as usual; otherwise typical of the genus. Palp: all segments except tarsus simple and without special modifications; tarsus inflated and extended as a long, curved embolus (Fig. 30) not seen elsewhere in the genus. Abdomen: 1.1 mm long; 0.59 mm wide; ovoid in general; spinnerets as usual in the genus; scuta are very poorly outlined. Color in alcohol: carapace with the usual yellowish brown color; sternum and legs somewhat lighter; abdomen very light yellowish white with numerous, small, irregular, white, glistening flecks.

Diagnosis. This species also appears to belong to the group of species represented by *Stenoonops portoricensis* Petrunkevitch, but the palp is very distinctive and plainly establishes it as a new species.

Records. The female is unknown and there are no male paratypes.

Stenoonops petrunkevitchi Chickering
Figures 31-33

Stenoonops petrunkevitchi Chickering, 1951: 241, figs. 29-30. The male holotype from Barro Colorado Island, Panama Canal Zone, July, 1938, is in the Museum of Comparative Zoology.

Female. There is no certainty that the female described here belongs in this species. It seems reasonable, however, to make this assumption because of the close resemblance to the male and because no other species have been reported from this region as far as I have been able to learn. Total length 1.37 mm. Carapace 0.61 mm long; 0.44 mm wide opposite posterior borders of second coxae where it is widest; 0.20 mm tall; somewhat raised just behind PME and then level along midline to beginning of fairly steep posterior declivity opposite anterior border of third coxae; surface finely granular; dorsal surface with a double row of dark hairs all directed toward the midline (Figs. 31-33). Eyes: six in a compact group; apparently very near to those of male but outlines are indistinct. Chelicerae essentially as in male. Maxillae: nearly parallel; somewhat widened distally; about twice as long as lip. Lip: about as wide distally as at base; sternal suture appears nearly straight. Sternum: essentially as in male; third and fourth coxae nearly globose; first and second somewhat elongated. Legs: essentially as in male. Abdomen: essentially as in male; scuta barely visible; epigynal area without distinctive features.

Records. The described female is from Barro Colorado Island, Panama Canal Zone, August 16, 1954. Since the male holotype was collected in July, 1938, the following specimens have been added to the collection: two males taken on Barro Colorado Island, February 8, 1958; two males taken in the Panama Canal Zone Forest Preserve, January 6, 1958. One male collected by Dr. A. M. Nadler on Barro Colorado Island, April, 1953, is also referred to this species. Apparently this species is not abundant in regions of Panama where I have collected. What is probably an immature female from the Canal Zone Forest Preserve, July 23, 1950, may represent a new species.

Stenoonops hoffi sp. nov.
Figures 34-42

Holotype. The male holotype is from Jamaica, W. I., St. Thomas Parish, Morant Point, May 6, 1956. Collected by Dr. C. C. Hoff

from axils of thatch palm. The species is named after the collector.

Description. Total length 1.14 mm including extended spinnerets; excluding the spinnerets, total length is 1.06 mm. Carapace 0.51 mm long; 0.38 mm wide opposite second coxae where it is widest; 0.18 mm tall; sharply narrowed opposite PLE; gently arched along midline from PME to beginning of steep posterior declivity; broad median region from PME to beginning of posterior declivity smooth and shining; lateral and posterior surfaces irregularly granular; with ventral margin finely serrated; few hairs or bristles observed except in ocular region where there are several stiff bristles (Figs. 34-35). Eyes: six as usual in a compact group; viewed from above, posterior row moderately recurved and wider than anterior row in ratio of about 5 : 4; posterior row occupies nearly the entire width of carapace at that level. Ratio of ALE : PME : PLE = 6 : 5 : 4.5. ALE bright silvery; separated from one another by nearly one-fourth of their long axis; only slightly oval; separated from PME by about one-sixth of their long axis and from PLE by a line; with considerable black pigment in ocular area. Clypeus somewhat porrect; with several spiniform bristles; height equal to about three-fourths of the long axis of ALE (Fig. 36). Chelicerae: vertical; parallel; apparently without special modifications. Maxillae: long, slender, convergent and touching beyond lip. Lip: much wider than long; otherwise typical of the genus. Sternum: quite convex; surface smooth through narrow median region but elsewhere irregularly granulate; quite plainly lobed and grooved along lateral margins; longer than wide in ratio of about 5 : 4; widest opposite interval between second and third coxae but nearly as wide between first and second coxae; third and fourth coxae subglobose, others somewhat elongated; posterior end bluntly terminated but apparently slightly bilobed; extended between bases of fourth coxae which are separated by nearly 1.5 times their width. Legs: 4123 in order of length; no true spines observed. Palp: tarsus inflated as usual with terminal features difficult to observe but apparently distinctive (Figs. 37-40); femur, patella, and tibia simple and without special modifications. Abdomen: regularly ovoid; spinnerets somewhat extended beyond tip of abdomen; about two-thirds as wide as long; epigastric and narrow ventral scuta moderately well outlined (Fig. 41). Color in alcohol: carapace brown with irregular streaks on lateral and posterior surfaces caused by the granulations previously referred to; sternum somewhat lighter brown; legs and mouth parts yellowish with variations; coxae darker; abdomen yellowish and with considerable iridescence; scuta somewhat darker.

Female paratype. Total length, exclusive of the slightly extended spinnerets 1.21 mm. Carapace 0.54 mm long; 0.4 mm wide; nearly 0.19 mm tall. Otherwise the briefly described female paratype appears to be essentially almost identical to the male in nearly all features. Even the abdominal scuta and epigynal area differ only slightly from corresponding regions of the male (Fig. 42).

Diagnosis. This species seems to be closely related to *Stenoonops minutus* Chamberlin and Ivie, now known from Florida and South Bimini, Bahama Islands. It differs from that species in respect to color pattern and the minute and obscure features of the male palpal tarsus.

Records. The described female paratype is from Jamaica, W. I., St. Thomas Parish, Morant Point, Oct. 14, 1957; taken from palm debris on the ground. Two male paratypes were taken with the holotype. Two female paratypes are in the collection from Trelawney Parish, fourteen miles east of Falmouth, May 15, 1956 (C. C. Hoff), and one additional female is from St. Catherine Parish, Guanaboa Vale, December 4, 1957.

Stenoonops minutus Chamberlain and Ivie

Stenoonops minutus Chamberlin and Ivie, 1935: 8, figs. 1-2, 14. The male holotype from Tampa, Florida, U. S. A., is now on semipermanent loan from the Museum of the University of Utah in the American Museum of Natural History, New York City, N. Y., examined. Roewer, 1942: 280; Bonnet, 1958: 4156; Chickering, 1969 (in press).

Several specimens of both sexes on loan from the American Museum of Natural History have been assigned to this species. All of these were collected on South Bimini, Bahama Islands, B. W. I., as follows: May, 1951 (W. J. Gertsch and M. A. Cazier); June, 1951 (M. A. Cazier and C. and P. Vaurie); July, 1951 (C. and P. Vaurie); April, 1952 (E. Mayr); December, 1952 and March, 1953 (A. M. Nadler). For some time these specimens were regarded as representing a new species and were described as such. Following a comparison with specimens of *Stenoonops minutus* Chamberlin and Ivie from Florida, they have now been assigned to that species. Minor differences have been noted but they are now regarded as well within the range of normal variation within a species.

Stenoonops phonetus sp. nov.

Figures 43-46

Holotype. The male holotype is from Puerto Rico, Cidra, Treasure Island, February 26-27, 1955; collected by Dr. A. M. Nadler.

It will be deposited in the American Museum of Natural History, New York, N. Y. The name of the species is an arbitrary combination of letters.

Description. Total length 1.19 mm. Carapace 0.55 mm long; nearly 0.39 mm wide opposite second coxae where it is widest; nearly 0.20 mm tall; raised considerably just behind PME and then nearly level to beginning of steep posterior declivity opposite anterior borders of third coxae (Figs. 43-44); without a median thoracic groove or pit; central regions smooth with few hairs; lateral and posterior surfaces irregularly granulate; ventral margins plainly serrated. Eyes: six in two rows as usual; in a compact group nearly as broad as the carapace at that level; posterior row gently recurved and wider than anterior row in ratio of nearly 7 : 6. Ratio of eyes ALE : PME : PLE = 12 : 11 : 10. PME considerably longer than wide; some irregularities in outlines of eyes noted. ALE separated from one another by nearly one-third of their diameter; separated from PME only by a line and contiguous to PLE; PME contiguous for nearly one-third of their circumference and contiguous to PLE for only a short distance. Clypeus considerably porrect; height equal to nearly two-thirds of the long diameter of ALE; with several quite long, slender spines. Chelicerae, maxillae, and lip quite typical of the genus as far as observed. Sternum: quite conspicuously lobed and grooved; longer than wide in ratio of nearly 4 : 3; widest just behind second coxae where a lobe extends laterally; posterior end terminates just opposite bases of fourth coxae which are separated by somewhat more than their width; surface very finely granulate. Legs: 41=23 in order of length; true spines are lacking as usual. Palp: typical of several species in the genus with features very inconspicuous (Fig. 45); a jet of semen is very conspicuous, however. Abdomen: quite typical of the genus; with epigastric and ventral scuta fairly well outlined and essentially as in female; with internal sacs just anterior to spinnerets on the venter showing through fairly clearly. Color in alcohol: carapace a medium brown with irregular darker patches along lateral and posterior surfaces caused by granulations; only a moderate amount of black pigment in ocular area; sternum a somewhat lighter yellowish brown; legs and mouth parts yellowish with little variation; palpal tarsus white.

Female paratype. Total length 1.29 mm. Carapace nearly 0.55 mm long; nearly 0.40 mm wide just behind second coxae where it is widest; general shape and other features essentially as in male; with ventral border serrated as in male. Eyes: essentially as in male but occupying a little less of the width of the carapace; ALE separated

a little further from PME than in the male; otherwise spaced essentially as in that sex; clypeus equally porrect and fully as tall as in male. Chelicerae: very finely rugulose in front; otherwise essentially as in male. Maxillae and lip also essentially as in male. Sternum: longer than wide in ratio of about 17 : 14; somewhat less conspicuously grooved and lobed than in male; extends to just opposite bases of fourth coxae which are separated by nearly five-fourths of their width. Legs essentially as in male. Abdomen: essentially typical of females of the genus; epigastric and ventral scuta moderately well outlined (Fig. 46); paired dark sacs anterior to spinnerets fairly well outlined. Color in alcohol essentially as in male.

Diagnosis. This species seems to be closely related to *Stenoonops minutus* Chamberlin and Ivie now known from Florida and South Bimini, Bahama Islands, and for a time was included with that species. A careful comparison, however, seems to show that it differs from that species significantly with respect to the following features: relative position of the eyes; appearance of the clypeus; shape of the carapace; and, especially, in respect to the conspicuously serrated ventral border of the carapace (Figs. 43-44).

Records. The described female paratype is from Mayagüez, Puerto Rico, January 19, 1955. In addition to the holotype and the described female paratype, I have had the following specimens for study: one male taken with the described female paratype; one female from Rio Piedras, March 14, 1959; two males from Rio Piedras, Humacao Co., March 2, 1955. All of these are from Puerto Rico and all were collected by Dr. A. M. Nadler. All specimens mentioned here will be deposited in the American Museum of Natural History, New York, N. Y.

Stenoonops scabriculus Simon

Figures 47-48

Stenoonops scabriculus Simon, 1891: 565. The holotype male from St. Vincent, B. W. I., is in the British Museum (Natural History), examined. Simon, 1892: 447; 1893: 296; Petrunkevitch, 1911: 129; 1928: 87; Roewer, 1942: 280; Bonnet, 1958: 4156.

The male from St. Vincent, B. W. I., is the type species of the genus. The original description was very briefly given in Latin and was not accompanied by figures. A male, believed to be the holotype, was loaned for study from the British Museum (Natural History). The date accompanying this species, however, was given as 94-10-17.

Male holotype. Total length 1.39 mm, exclusive of the somewhat extended spinnerets and chelicerae; including these parts total length is 1.51 mm. Carapace 0.65 mm long; 0.43 mm wide; 0.2 mm tall; slightly arched along midline from PME to beginning of moderately steep posterior declivity; surface finely granular; with no indication of a median thoracic groove or pit; ventral margin finely serrated. Eyes: posterior row occupies nearly three-fifths of width of carapace at that level; only slightly wider than anterior row; moderately recurved (Fig. 47). Ratio of eyes ALE : PME : PLE = 6 : 5.75 : 5. ALE separated from one another by about one-third of their long axis; barely separated from PME and PLE. PME contiguous to one another for one-third of their circumference; separated from PLE by a line. Height of clypeus equal to slightly more than one-half the long axis of ALE. Chelicerae: nearly vertical; slightly extended; essentially parallel; with no special modifications observed. Maxillae: probably divided distally but fragility of specimen prevents close examination. Lip: hidden by numerous hairs but apparently without special modifications. Sternum: moderately lobed and grooved; surface finely granular; longer than wide in ratio of about 9 : 7; widest opposite interval between second and third coxae where well-developed lobes extend laterally; posterior end narrowed and bluntly rounded just opposite bases of fourth coxae which are separated by a little more than five-fourths of their width. Legs: 4123 in order of length; with few bristles and with no spines observed. Palp: femur of moderate length, both patella and tibia short; essential features of the tarsus shown in Figure 48; tarsus with numerous broad hairs on the cymbium and the usual dorsal pad of short, fine hairs. Abdomen: ovoid; 0.81 mm long; 0.5 mm wide a little behind the middle; spinnerets as usual in the genus; epigastric and ventral scuta hardly visible. Color in alcohol: carapace and sternum yellowish brown; only a small amount of black pigment in ocular area; legs and mouth parts lighter than carapace and sternum with variations; abdomen very light yellowish.

Records. Simon reported this species from Venezuela as well as from St. Vincent, B. W. I. I failed to collect the species during my visit to this island in 1966 and, as far as I have been able to determine, it has not been reported since the holotype was taken.

STENOONOPS HALATUS sp. nov.

Figures 49-52

Holotype. The female holotype is from Antigua, B. W. I., Fig Tree Hill, near Old Road, August, 1967. Collected by Mrs. Elsa

Sabath. The name of the species is an arbitrary combination of letters.

Description. Total length 1.62 mm exclusive of the slightly extended spinnerets (Fig. 49); including the spinnerets total length is 1.67 mm. Carapace about 0.61 mm long; about 0.5 mm wide opposite posterior border of second coxae where it is widest; about 0.27 mm tall; raised slightly just behind PME and continues to rise somewhat to beginning of steep posterior declivity (Fig. 50) nearly opposite third coxae; surface finely granular and with few hairs. Eyes: six as usual in a compact group; posterior row moderately recurved and occupying slightly more than three-fourths of width of carapace at that level and wider than anterior row in ratio of about 6 : 5. Ratio of eyes ALE : PME : PLE = about 8 : 7 : 6.5. ALE separated from one another by somewhat less than one-half their radius; barely separated from PLE and separated from PME by only a line. PME contiguous for about one-fourth of their circumference and nearly contiguous to PLE for only a short distance; with a moderate amount of black pigment in ocular area. Clypeus quite porrect and with height nearly equal to radius of ALE; with several spiniform bristles (Fig. 51). Chelicerae, maxillae, and lip essentially typical of females of the genus. Sternum: obscured by curled, fragile legs; apparently quite typical of the genus; longer than wide in ratio of about 19 : 15; quite distinctly lobed and grooved; slightly bilobed at posterior end, which is just opposite the middle of the fourth coxae, which are separated by slightly less than 1.5 times their width. Legs: 42=13 in order of length; no true spines observed; all legs moderately long and slender. Palp with many fine hairs and bristles. Abdomen: ovoid; longer than wide in ratio of nearly 4 : 3; epigastric and ventral scuta quite clear and typical of the genus (Fig. 52). Spinnerets also quite typical of the genus. Color in alcohol: carapace a light yellowish brown with somewhat darker areas corresponding to uneven distribution of granulations; sternum nearly like carapace; legs and mouth parts yellowish with some variations; abdomen nearly white in general, with faint reticulations; scuta light yellowish brown with variations; just anterior to the base of the anterior spinnerets a pair of darker, irregular spots occur as usual in the genus; there are also many short, black hairs on this part of the body.

Diagnosis. This species seems to be most closely related to *Stenoonops reductus* (Bryant) but it differs considerably from that species with respect to the shape of the carapace, features of the sternum, and characteristics of the scuta and epigynal area.

Records. The male is unknown and there is no female paratype.

Stenoonops reductus (Bryant)
Figures 53-58

Scaphioides reducta Bryant, 1942: 327, pl. 1, figs. 6, 8. The female holotype from St. Croix, U. S. Virgin Islands, is in the Museum of Comparative Zoology, Harvard University, Cambridge, Mass., examined.

Miss Bryant apparently regarded this species as a close relative of the species placed in the genus *Scaphiella* Simon and erected a new genus for it. I am obliged to consider the species as belonging to the genus *Stenoonops* Simon and am placing it here on the basis of the appearance of the male palp, the ventral scuta, eyes, sternum, and general form of the whole body. A male from St. Croix, U. S. V. I., has been selected for rather detailed description as given below.

Male. Total length 1.56 mm exclusive of the somewhat extended spinnerets; including the spinnerets total length is 1.61 mm. Carapace 0.64 mm long; 0.5 mm wide opposite second coxae where it is widest; 0.26 mm tall; gently arched from PME to beginning of steep posterior declivity; surface notably granular which gives the ventral margin a finely serrated appearance; with no evidence of a median fovea or groove (Figs. 53-54). Eyes: six as usual in a compact group; posterior row gently recurved and occupying fully two-thirds of width of carapace at level of posterior border of PLE. Ratio of eyes ALE : PME : PLE = 12 : 11 : 10. ALE narrowly separated from one another and separated from PME and PLE by about one-seventh of their long axis. PME contiguous for nearly one-third of their circumference and contiguous to PLE for a short distance. Clypeus quite porrect; height of clypeus nearly equal to long axis of ALE. Chelicerae, maxillae, and lip essentially as described for the holotype female; with no special modifications observed. Sternum: convex; only a little longer than wide just behind second coxae where it is widest; considerably narrowed in front; surface granular with sharply accentuated marginal lobes and grooves; a rounded lobe at posterior end between bases of fourth coxae, which are separated by about seven-fifths of their width; third and fourth coxae subglobose; first and second coxae slightly more elongated. Legs: 41=23 in order of length; numerous short hairs on all legs but no spines observed. Palp: femur of moderate length, about twice as long as patella; both patella and tibia short; tarsus with distinctive features (Figs. 55-56). Considerable variation has been noted among the available males in respect to length of terminal palpal tarsal structures.

Abdomen: ovoid in general; 0.88 mm long exclusive of the somewhat extended spinnerets; 0.61 mm wide near middle; epigastric and narrow ventral scuta are well developed (Fig. 57) and chitinized essentially as described for the female holotype except that both scuta are closely pressed together. Color in alcohol: carapace a rich medium brown somewhat lighter along median region and with a moderate amount of black pigment in ocular area; sternum nearly like carapace; mouth parts and legs yellowish with variations; abdomen nearly white with scuta clearly delineated and colored nearly like sternum. Epigynal area of female somewhat distinctive (Fig. 58).

Records. The described male is from St. Croix, U. S. Virgin Islands, Frederiksted, March 23, 1964. Numerous specimens of both sexes are in the collection from several localities in the vicinity of Frederiksted and King's Hill, March, 1964, and September, 1966. Two males and a female were taken on St. John, U. S. Virgin Islands, March, 1964.

Stenoonops noctucus sp. nov.

Figures 59-63

Holotype. The male holotype is from St. Thomas, U. S. Virgin Islands, taken from hay and weed debris on roadside in outskirts of Charlotte Amalie, February 9, 1964. The name of the species is an arbitrary combination of letters.

Description. Total length exclusive of the slightly extended chelicerae and spinnerets 1.19 mm; including these structures total length is 1.28 mm. Carapace 0.5 mm long; 0.38 mm wide just behind second coxae where it is widest; 0.14 mm tall (slightly lower than usual); nearly level along midline from PME to beginning of moderately steep posterior declivity; surface smooth and with no evidence of a median thoracic groove or pit. Eyes: unusual in the genus; six in a compact group; posterior row slightly procurved and occupying nearly three-fifths of width of carapace at that level. Ratio of eyes ALE : PME : PLE = nearly 4.5 : 5 : 4. Outline of eyes somewhat irregular and difficult to observe especially with respect to PME (long axes used for measurements). ALE separated from one another by nearly three-eighths of their long axis; separated from PME by about three-sixteenths of their long axis and from PLE by only a line. PME unusually elongated (Fig. 59) and contiguous for nearly their long axis and contiguous to PLE for about one-fourth of the long axis of the latter; some asymmetry of eyes noted. Clypeus very narrow; apparently its

height is not more than one-fourth of the long axis of ALE. Chelicerae: slender, vertical; of moderate length. Maxillae: slightly convergent; about twice as long as lip, which is about as long as wide at base. Sternum: moderately raised and then nearly flat; longer than wide in ratio of about 7 : 6; widest between second and third coxae where a lobe extends laterally and bears a cluster of stiff, curved bristles (Fig. 60); not otherwise conspicuously lobed or grooved; surface smooth with numerous short hairs or bristles generally curved inward; bluntly rounded posterior end extends just to base of fourth coxae, which are separated by about five-fourths of their width; third coxae globose, fourth subglobose, others somewhat elongated. Legs: 4123 in order of length; with many stiff hairs and spiniform bristles but no true spines. Palp: femur somewhat elongated; patella and tibia short; tarsus inflated and with very obscure but quite distinctive features (Figs. 61-63). Abdomen: elongate ovoid; spinnerets of moderate length; epigastric and ventral scuta only weakly indicated; with many short, dark, stiff hairs. Color in alcohol: carapace and sternum a light yellowish brown; legs and mouth parts somewhat lighter; abdomen with several irregular, purplish spots of different sizes against a nearly white dorsal background; venter nearly white with a pair of yellowish spots just anterior to the spinnerets.

Female paratype. Total length 1.34 mm. Carapace 0.55 mm long; 0.41 mm wide; 0.15 mm tall. Eyes essentially as in male. Chelicerae, maxillae, and lip also essentially as in male with minor differences considered unnoteworthy. Palp with many stiff, conspicuous bristles. Sternum essentially as in male with the conspicuous lateral lobes extended between second and third coxae. Legs also essentially as in male. Abdomen: with epigastric and ventral scuta faintly visible; epigynal area indistinguishable. Color in alcohol: cephalothorax and appendages as in male; abdomen with the purplish spots somewhat more clearly shown than in male; in the anterior third of the dorsum are two pairs of somewhat irregular purplish spots and in the posterior third of the dorsum there is a pair of larger purplish spots; on the venter just anterior to the spinnerets there is a pair of somewhat oval, brownish spots; elsewhere the abdomen is a very light yellowish.

Diagnosis. This species appears to exhibit many of the usual generic characters of *Stenoonops* but does not seem to be closely related to any other species in the genus as I have come to know it. The eyes, features of the sternum, and color pattern all seem to indicate that this species represents a new group to add to the

genus. In the past it might very well have been assigned to a new genus by some taxonomists.

Records. The described female paratype, together with two additional females, were all taken from hay and weed litter on the roadside close to the spot that yielded the male holotype on February 9, 1964. One female was taken on St. John, U. S. Virgin Islands, Cruz Bay, March 1, 1964.

Stenoonops padiscus sp. nov.

Figures 64-68

Holotype. The male holotype is from Jamaica, W. I., St. Catherine, three miles east of May Pen, November 22, 1957. The name of the species is an arbitrary combination of letters.

Description. Total length about 1.25 mm (the holotype is very fragile and somewhat dismembered) exclusive of the extended spinnerets and chelicerae; including these structures, total length is about 1.36 mm. Carapace 0.52 mm long; 0.37 mm wide just behind second coxae where it is widest; about 0.19 mm tall; ventral margin somewhat irregular but not definitely serrated as in some species; continues from PME nearly level to beginning of very gradually descending posterior declivity; surface very finely granulate; hairs along medial region convergent toward midline. Eyes: six in a compact group; posterior row occupies about six-elevenths of width of carapace at that level; posterior row somewhat procurved, measured by posterior borders and viewed from above. Ratio of eyes ALE : PME : PLE = nearly 5 : 5 : 4 (long diameters used for measurements). PME much narrowed (Fig. 64); only about half as wide as long. ALE separated from one another by about three-tenths of their diameter; barely separated from PLE and separated from PME by less than one-fifth of their diameter. PME contiguous for fully one-third of their circumference; barely separated from PLE. Posterior row of eyes only a little wider than anterior row. Height of clypeus somewhat less than radius of ALE. Chelicerae, maxillae, and lip apparently typical of the genus. Sternum: widest near middle where a lateral lobe extends between second and third coxae; only longer than wide at this point in ratio of about 6 : 5; with practically no marginal grooves; with numerous bristles especially along margins; sternal suture at base of lip nearly straight; posterior end extended between bases of fourth coxae which are separated by nearly five-fourths of their width. Legs: 4123 in order of length; no spines observed; trichobothria

observed but exact number and placement not determined. Palp: only tarsus with special modifications (Figs. 65-67). Abdomen: essentially typical of the genus except that the scuta and genital region are very obscurely outlined and not suitable for illustration. Color in alcohol: carapace, sternum, legs, and mouth parts a pale yellowish with variations; abdomen nearly white with variations.

Female paratype. Although no females were taken with either male assigned to this species, it seems reasonable to assume that this specimen represents the female of the species because of its close resemblance to the holotype. Total length 1.43 mm exclusive of the somewhat extended chelicerae and spinnerets; including these structures, total length is about 1.54 mm. Carapace about 0.57 mm long; 0.42 mm wide opposite posterior border of second coxae where it is widest; nearly 0.21 mm tall; slightly arched along midline from PME to beginning of moderately steep posterior declivity nearly opposite interval between second and third coxae; no serrations observed along ventral border. Eyes: essentially as shown in Figure 68; very similar to those of male; all eyes quite silvery. Chelicerae, maxillae, and lip essentially as usual in the genus. Sternum: longer than wide in ratio of about 4 : 3; widest opposite interval between second and third coxae where a conspicuous lobe extends laterally as in male; moderately lobed but without grooves; with many incurved bristles especially along margins; sternal suture straight; posterior end extended between fourth coxae which are separated by about 1.2 times their width. Legs: essentially as in male. Abdomen: ovoid as usual; generally typical of the genus except that the scuta and epigynal area are barely discernible and without distinctive features. Color in alcohol: essentially as in male except that the abdomen is yellowish white with a faint darker reticulation more evident on dorsum than on venter.

Diagnosis. In my judgment, this species is another somewhat aberrant member of the genus, closely related to *Stenoonops noctucus* sp. nov. but somewhat remotely related to other species that I have had an opportunity to study.

Records. The described female paratype is from Jamaica, W. I., St. Thomas, Morant Point, Maumee Bay, October 14 ,1957. In addition to these two specimens, my collection contains the following specimens, all from Jamaica, W. I.: one male from St. Andrew Parish, Newcastle Road, five miles from Kingston, May 10, 1950 (C. C. Hoff); three females from St. Catherine Parish, two miles east of Ferry, May 17, 1956 (C. C. Hoff); St. Andrew Parish, Ferry, one mile west of Red Hills Road, Oct. 6, 1957; St. Thomas Parish, Morant Point, May 6, 1956 (C. C. Hoff).

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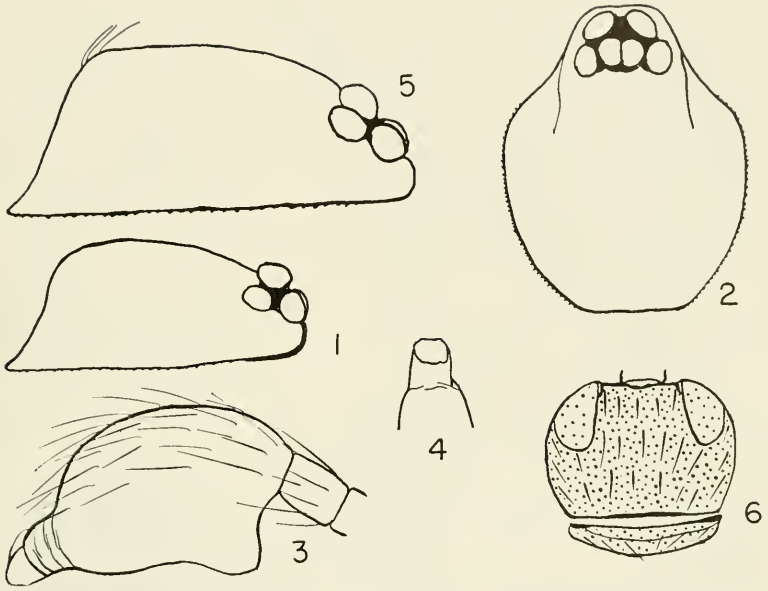
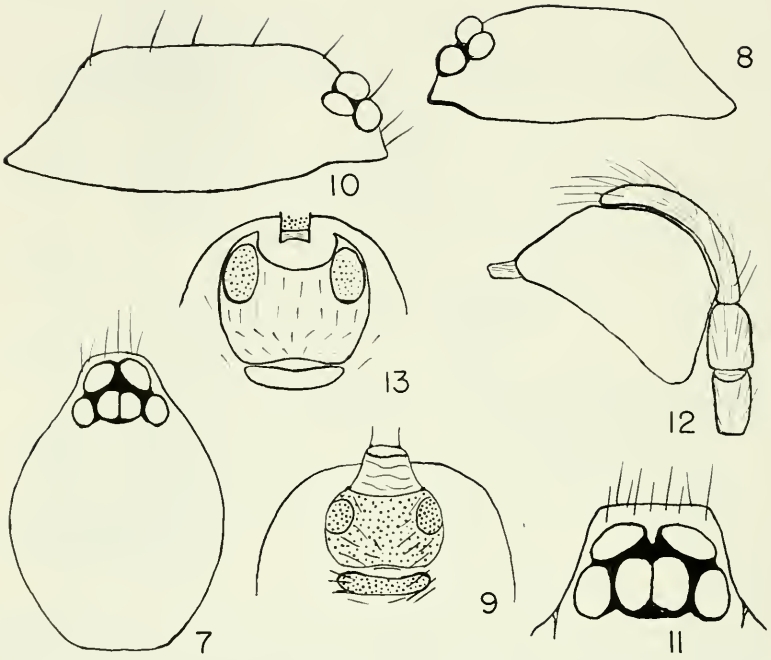


Figures 1-6. *Stenoonops cletus* sp. nov. Fig. 1, Carapace of male; right lateral view. Fig. 2, Carapace of male from above. Fig. 3, Left palpal tibia and tarsus; retrolateral view. Fig. 4, Distal end of palpal tarsus; nearly ventral view. Fig. 5, Carapace of female; right lateral view. Fig. 6, Epigastric and ventral scuta of female from below.



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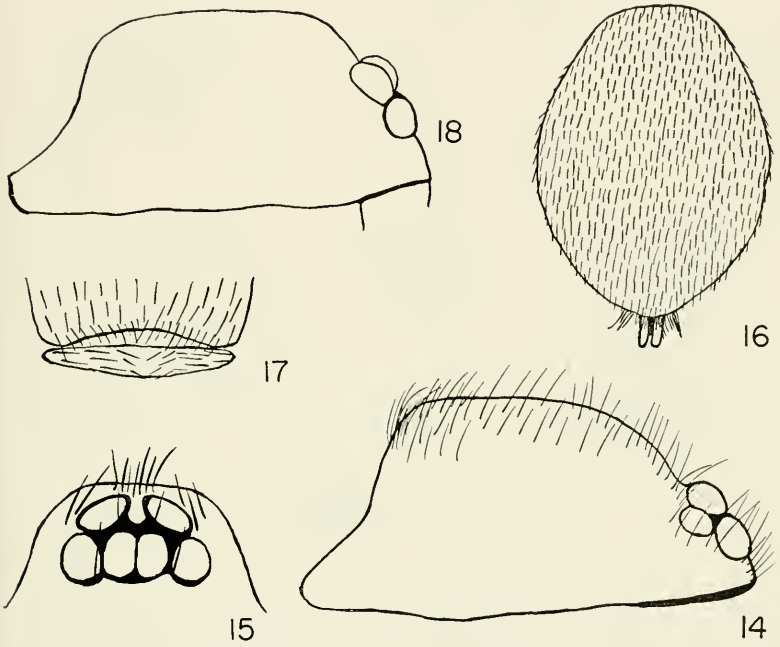

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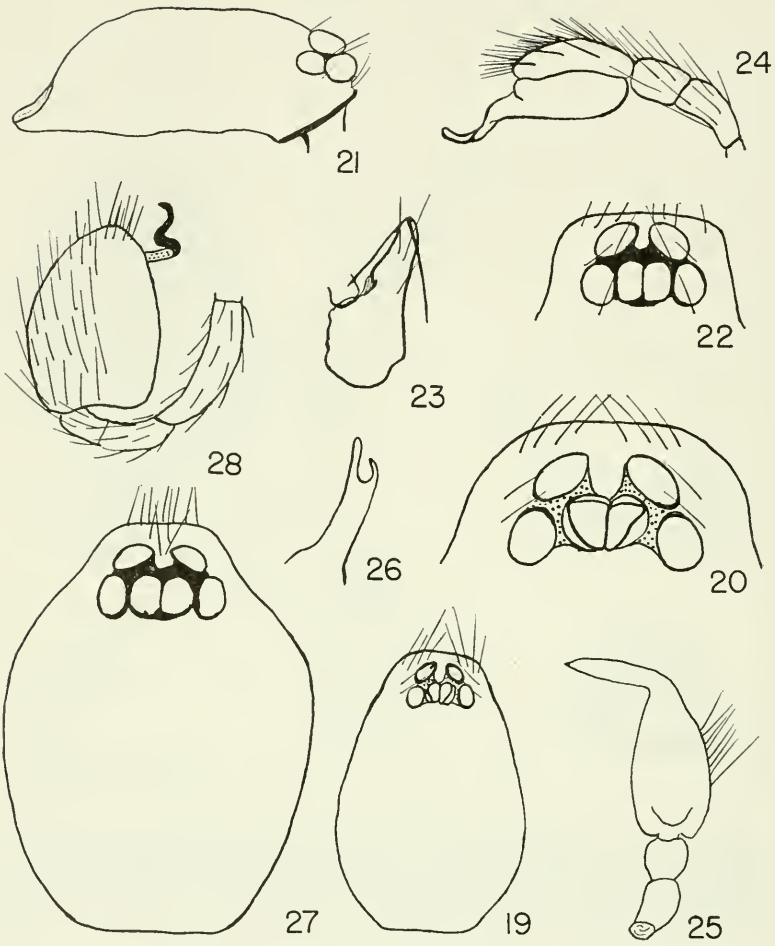
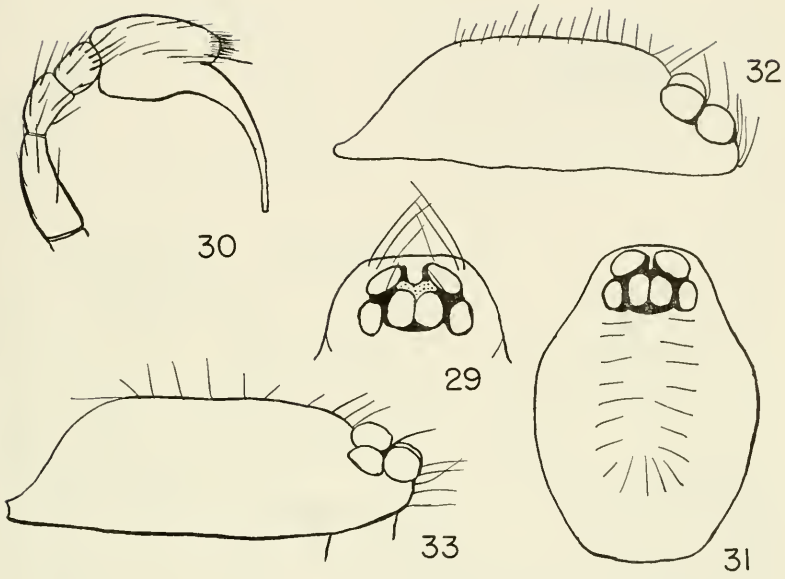


Figs. 19-20. *Stenoonops dimotus* sp. nov. Fig. 19, Carapace of holotype from above. Fig. 20, Eyes of holotype from above. Figs. 21-26. *Stenoonops insolitus* sp. nov. Fig. 21, Carapace of male holotype right lateral view. Fig. 22, Eyes of holotype from above. Fig. 23, Right maxilla from dissected male paratype. Figs. 24-25, Left palp of holotype; retrolateral and nearly ventral views, respectively. Fig. 26, Distal end of palpal tarsus; more enlarged and turned to show division. Figs. 27-28. *Stenoonops lucradus* sp. nov. Fig. 27, Carapace of holotype male from above. Fig. 28, Left palp of male holotype; prolateral view.



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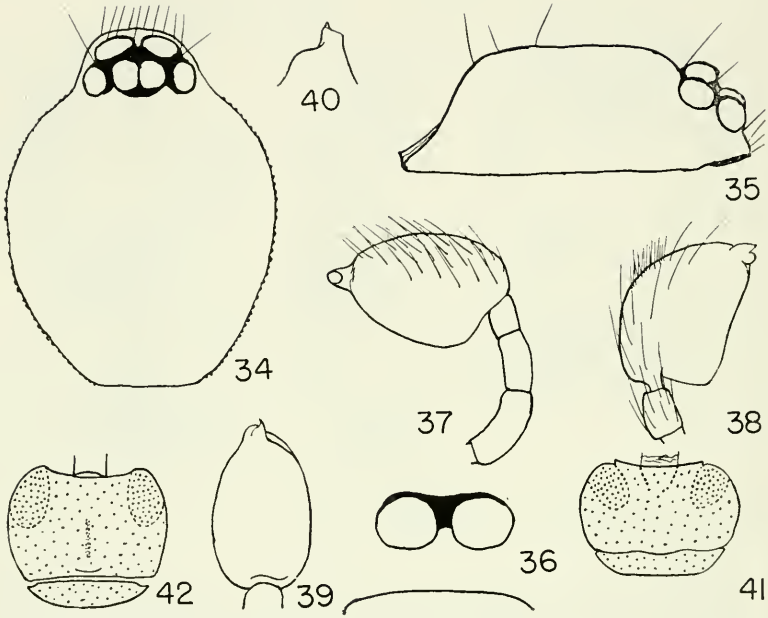

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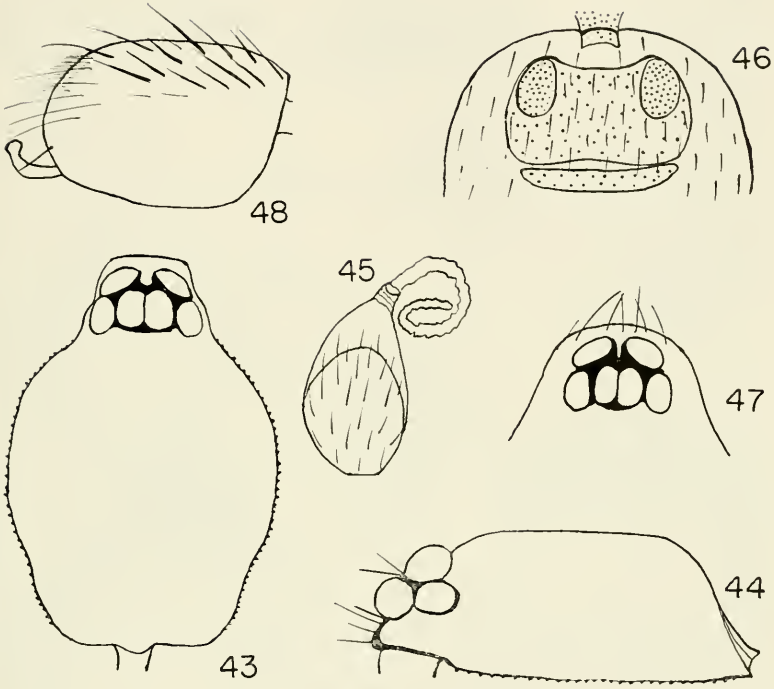

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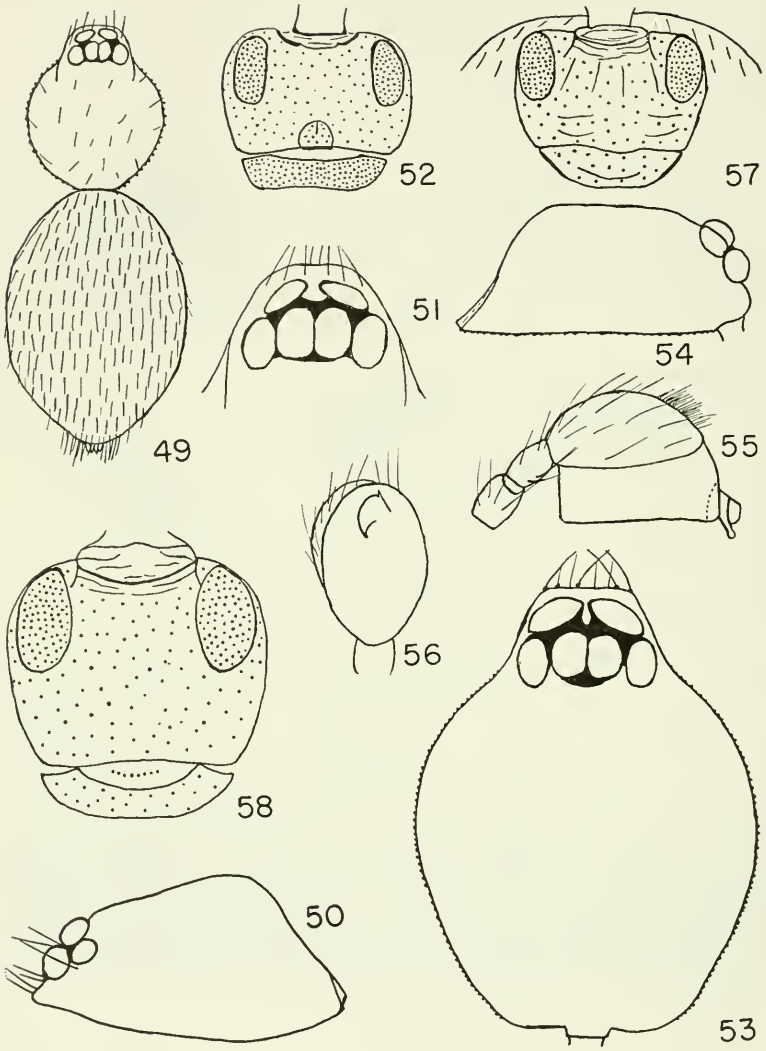
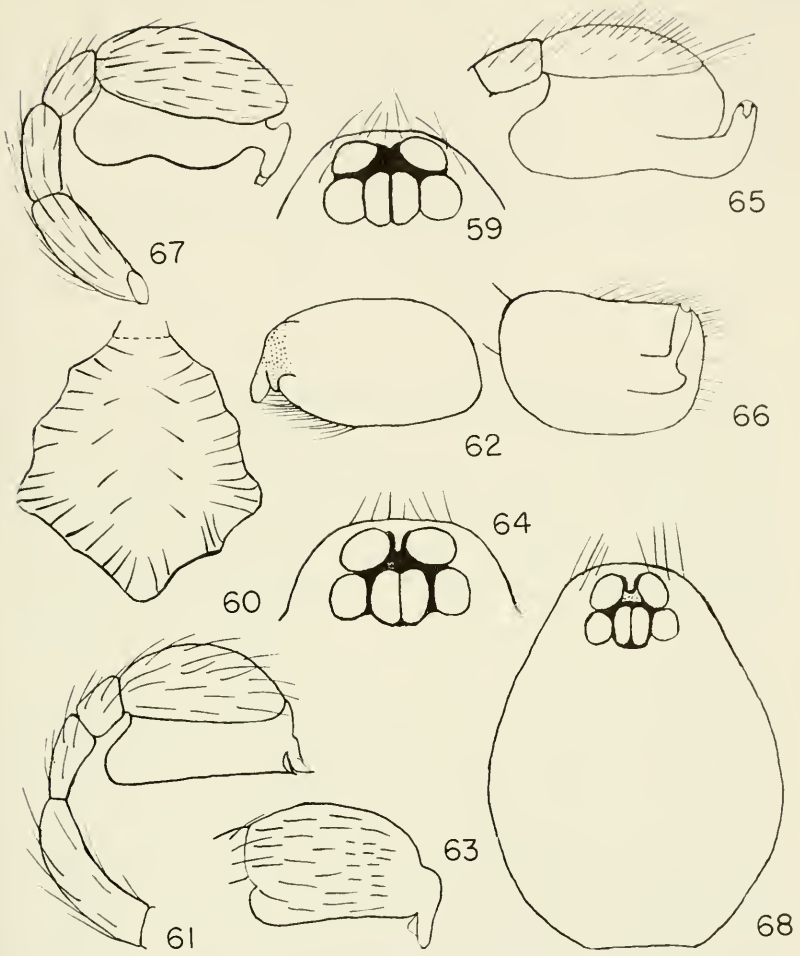


Figs. 49-52. *Stenoonops halatus* sp. nov. Fig. 49, Body of female holotype from above. Fig. 50, Carapace of holotype; left lateral view. Fig. 51, Eyes of holotype from above. Fig. 52, Abdominal scuta and epigynal area of holotype from below. Figs. 53-58. *Stenoonops reductus* (Bryant). Fig. 53, Carapace of male from above. Fig. 54, Carapace of male; right lateral view; lower magnification. Fig. 55, Patella, tibia, and tarsus of left male palp; prolateral view. Fig. 56, Left palpal tarsus from below. Fig. 57-58, Epigastric and ventral scuta of male and female, respectively, from below.



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DISTRIBUTION OF THE CENTROLOPHID FISH *SCHEDOPHILUS PEMARCO*, WITH NOTES ON ITS BIOLOGY[1]

Richard L. Haedrich[2] and Fernando Cervigón[3]

ABSTRACT. *Schedophilus pemarco* is a non-schooling, somewhat rare fish that occurs along the West African coast from 19°N to 17°S on the bottom at depths of 50-250 m. In two different years, a solitary specimen has been taken in the southeast Caribbean; these specimens were probably wafted from West Africa via the North Equatorial Current. *S. pemarco* can be distinguished from other *Schedophilus* by the anal count of III 16-19 and the irregular horizontal stripes on the sides. Allometry is not particularly marked between 80 and 240 mm SL. Fishes of 200 mm SL could be sexed, but were immature. Food items may include jellyfish, hyperiid amphipods, euphausiids, and small fish.

Schedophilus pemarco (Poll, 1959) is a near-shore fish of the tropical coast of West Africa. The type material, comprising four specimens, was from near the mouth of the Congo River (*ca.* 6°S) and from near Porto Amboin (*ca.* 11°S). Blache (1962) reported the species from the Gulf of Guinea, but gave no particulars as to the specimens on which the report was based. During the Guinean Trawling Survey (GTS), at least 14 more specimens were taken from off the mouth of the Kunene River (*ca.* 17°S) to Sierra Leone (*ca.* 8°N). This series and additional specimens from the "Walther Herwig" give a better impression of the species' distribution, and provide some information on the allometric growth and food habits of *Schedophilus pemarco*.

Although essentially a fish of the eastern tropical Atlantic,

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[2] Woods Hole Oceanographic Institution, Woods Hole, Mass., and Museum of Comparative Zoology, Harvard.

[3] Estacion de Investigaciones Marinas de Margarita, Nueva Esparta, Venezuela.

Schedophilus pemarco can range far from this area. This note reports two specimens, caught in different years, from off Venezuela in the southeastern Caribbean Sea.

Schedophilus pemarco (Fig. 1) is one of the most easily distinguished members of the genus. The low anal finray count (III 16-19) is the best diagnostic character. All other *Schedophilus* have at least 20 anal finrays, and one has as many as 40. The pattern of thin irregular horizontal stripes on the sides is another good distinguishing feature. Only *S. griseolineatus* (Norman) has a similar pattern, but this western South Atlantic species has 31-33 dorsal finrays in comparison to the 23-26 found in *S. pemarco.*

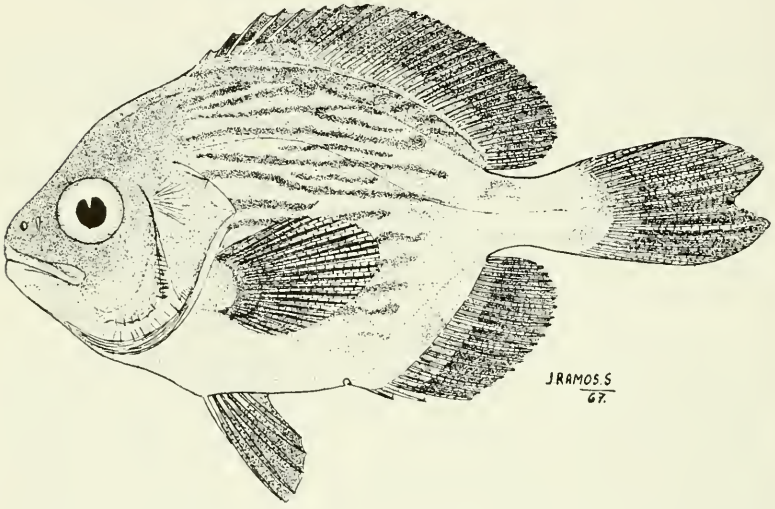

Fig. 1. *Schedophilus pemarco* (Poll), an 89-mm specimen from the Caribbean, 10°53.5′N 61°00.6′W. Museum of Comparative Zoology specimen.

Figure 2 shows the extent of allometric growth in *Schedophilus pemarco.* It is nowhere particularly marked, and, by the time the fish has reached a length of approximately 200 mm SL, the relative proportions are more or less stabilized and no longer change with growth. This is very generally the case in stromateoids, the most dramatic changes occurring early. In *S. medusophagus* (Cocco), for example, the greatest changes take place between 10 and 80 mm SL (Haedrich 1967: 47). Clearly, smaller specimens of *S. pemarco,* when found, may be expected to differ morphometrically from the ranges displayed by the larger specimens here reported.

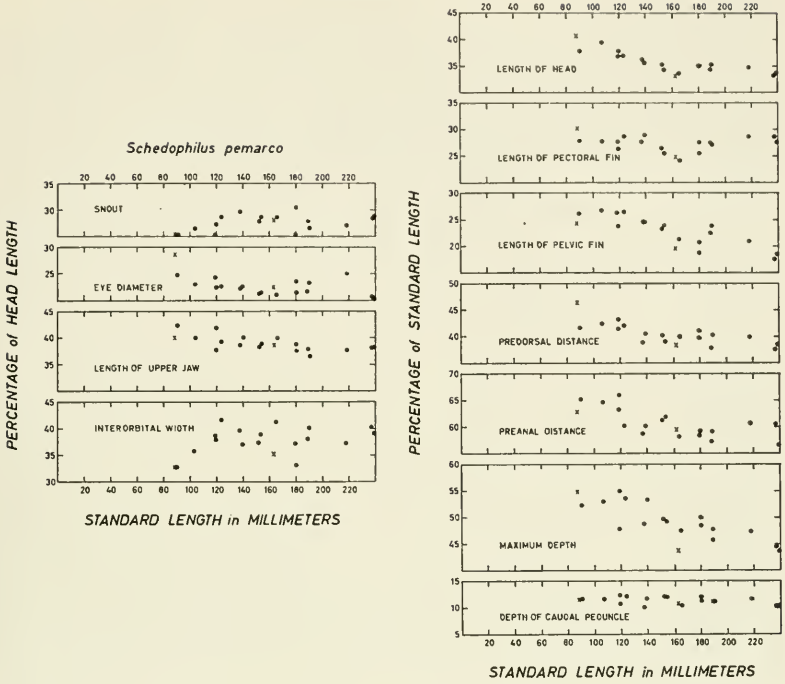

Fig. 2. Scatter diagram of the allometric growth in *Schedophilus pemarco*. • West African, x Caribbean.

The leveling off of the allometric growth curve may correspond approximately to the onset of maturity. Specimens of 200 mm SL could be sexed, though the gonads even in these were quite small and poorly developed. None of the specimens examined were mature. It is not likely that the failure to find fully developed gonads is merely a function of time of the year, since specimens in the material studied came from both spring and fall.

Stomachs were often empty. The most common food item encountered was the amorphous, soupy remains of jellyfish. In two stomachs, there were hyperiid amphipods about 5 mm long. Euphausiid remains were found on one occasion, and, in the stomach of a 152-mm fish, there was a 60-mm carangid fish, probably *Trachurus*.

All specimens were taken in bottom trawls. Figure 3 shows the depth of water in which each specimen was taken. Most of the catches (>60%) occurred in water shallower than 55 m. Plotted

against depth-of-capture in Figure 3 is the size of each specimen. The plot suggests that as *Schedophilus pemarco* grows larger, it seeks deeper water. All the specimens larger than 200 mm SL were taken at depths of 150 m or greater. This pattern of behavior is very commonly seen in the stromateoids, although in most cases the smaller fishes are pelagic, not bottom-living.

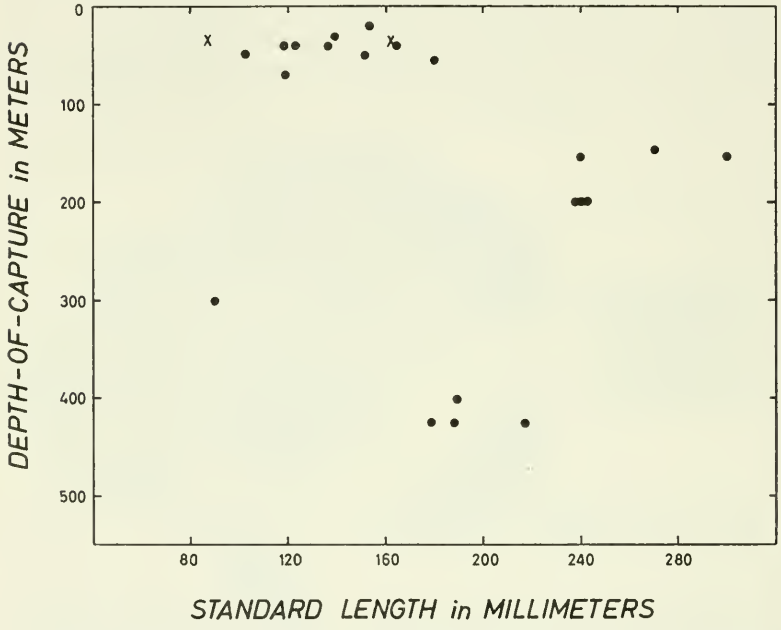

Fig. 3. Depth distribution of *Schedophilus pemarco*. Each point represents one specimen. All data from bottom trawls; when a depth range is indicated, only the mid-point is plotted. • West African, x Caribbean.

The bottom trawls used were of various sizes. The smallest was about 10 m across, the largest about 45 m. Those used by GTS were roughly 25 m. Despite these large trawls, most catches (>80%) were of single fish. The greatest number from any one trawl was three. *Schedophilus pemarco* is thus probably a non-schooling, somewhat rare, fish. The species was, for example, not abundant enough to enter into the analysis of species assemblages based on the 480 trawls of the GTS survey (Fager and Longhurst, 1968).

Figure 4 shows the horizontal distribution of *Schedophilus pemarco*. One of the northernmost records, at about 19°N, is from Cervigón (1960:69,74), where the fish was referred to as *Mupus sp. aff. M. ovalis*. The records along the African coast fall effectively within the 75°F isothere of Hutchins and Scharff (1947). Outside this region, the surface temperature is always colder than 75°F (24°C). Seasonal cooling, of course, reduces the surface temperature somewhat on each end of this distribution, but, for the most part, the temperature is always warmer than 18°C (Hutchins and Scharff, 1947). The 200-m temperature across this region, more or less stable the year around, ranges from about 10° to 15°C (Sverdrup *et al.*, 1942).

The two records of *Schedophilus pemarco* from the Caribbean, reported here for the first time, are of some interest. There can be no doubt as to the identification. The two fish almost certainly originated in Africa, and it is not hard to imagine the pathway that could be used, although the time needed seems somewhat long. Unpublished drift bottle data on file at the Woods Hole Oceanographic Institution suggests that the journey from the Mauretanian region to northeastern South America or the Lesser Antilles via the North Equatorial Current would take something of the order of six months. The Caribbean specimen illustrated in Figure 1 is one of the smallest *S. pemarco* known. Smaller specimens, as in

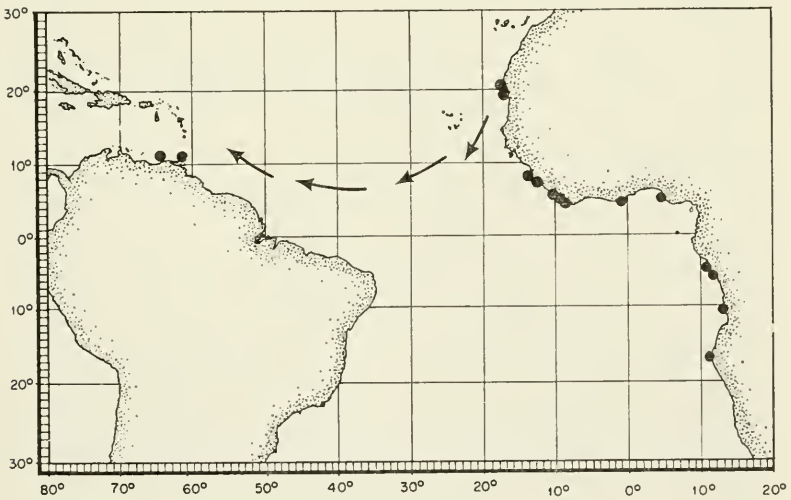

Fig 4. Geographical distribution of *Schedophilus pemarco*. The arrows indicate the general path of the North Equatorial Current.

other *Schedophilus,* may be pelagic and may associate with floating objects. If this is the case, as is likely, these fish would be prime candidates for transport.

Schedophilus pemarco does not seem to have established populations in the New World. It was not encountered, for example, in the extensive trawl surveys conducted during 1957-1959 on the continental shelf of British Guiana (Lowe, 1962), and continuous surveys both off the Guianas and in the southeastern Caribbean by Venezuela during 1962-1968 have taken only the specimens recorded here. Nonetheless, the taking of two specimens in each of two different years indicates that immigration from West Africa may occur with some regularity.

Transport and establishment are, of course, two quite different things. In comparison to the West African shore fish fauna, the fauna of the New World tropics is very rich indeed, and, in such a situation, one would expect the successful colonists to move from west to east. The data support this expectation. Briggs (1967) finds that no essentially West African fishes have been successful in crossing the Atlantic, but that over 100 species have established themselves in the opposite direction. Movement from west to east need not be an upstream movement, for there are zoogeographically important countercurrents in the equatorial region (Scheltema, 1968).

Description. Schedophilus pemarco is a deep-bodied, rather firm-fleshed fish. The profile of the head slopes steeply to the blunt snout. The head and nape lack scales. The preopercle is beset with 12-19 prominent spines. The large eye is centrally located, roughly one-half its diameter or more below the dorsal profile. The large mouth is inclined somewhat downward; the end of the maxilla extends to under the center of the eye or beyond. The pectoral fin is broad and rounded. The pelvic fins, inserted directly below the pectorals, are long and often reach beyond the anus. The color in preservative is grayish brown, with blue-gray-tinged horizontal lines running all along the sides. The fins are gray or blackish, darker than the body. The pelvics are particularly black. The head is uniformly dark with very dark, thin opercles, and the eye is bluish. In the summary of meristics which follows, the two numbers in parentheses are the figures for the two Caribbean specimens 88 and 162 mm SL respectively: in % SL — head 33-41 (41, 33), pectoral length 24-31 (30, 24), pelvic length 18-27 (24, 20), predorsal distance 38-47 (47, 38), preanal distance 57-66 (63, 60), maximum depth 43-55 (55, 44), least depth caudal peduncle 10-13 (12, 11); in % of head — snout 25-30

(26, 28), eye diameter 21-29 (29, 23), length upper jaw 39-43 (40, 39), interorbital width 32-42 (33, 35); counts — dorsal V-VII 23-26 (VI 24, VI 24), anal III 16-19 (III 16, III 17), pectoral 19-22 (21, 20), gill-rakers 5-7 + 1 + 13-16, most commonly 7 + 1 + 15 (7 + 1 + 15, 7 + 1 + 15), vertebrae always 10 + 15. Count frequencies for fin elements are given in Table 1.

Table 1. Count frequencies of fin elements in *Schedophilus pemarco*. Anal spines are III.

Dorsal spines	V	VI	VII	
Number of specimens	5	11	2	
Dorsal finrays	23	24	25	26
Number of specimens	3	12	3	1
Anal finrays	16	17	18	19
Number of specimens	1	11	7	1
Pectoral finrays	19	20	21	22
Number of specimens	1	7	11	1

Specimens used in this study, unless otherwise noted, are deposited in the Museum of Comparative Zoology, Harvard. Disposition of the others is in the Institut für Seefischerei, Hamburg (ISH); Museu de Historia Natural La Salle, Caracas (MHNC); or Tropical Atlantic Biological Laboratory, Bureau of Commercial Fisheries, Miami (TABL). Material examined: GTS — 1 spec. 90 mm SL, Geronimo 2-246, 9 Sept 63, 4°31′S 10°53′E, 300 m (TABL); 1 spec. 153 mm SL, Thierry 1-2, 21 Sept 63, 5°06′N 1°05′W, 20 m; 1 spec. 152 mm SL, La Rafale 18-4, 30 Oct 63, 4°35′N 8°25.5′W, 50 m; 1 spec. 189 mm SL, La Rafale 16-8, 4 Nov 63, 5°17′N 9°55′W, 400 m; 1 spec. 139 mm SL, La Rafale 15-2, 5 Nov 63, 5°55.5′N 10°12′W, 30 m; 1 spec. 119 mm SL, La Rafale 11-3, 15 Nov 63, 7°18.5′N 12°41′W, 40 m; 3 spec. 188-217 mm SL, La Rafale 11-8, 16 Nov 63, 7°12′N 12°46′W, 350-500 m; 3 spec. 123-165 mm SL, La Rafale 10-3, 17 Nov 63, 7°32′N 13°21′W, 40 m; 1 spec. 103 mm SL, La Rafale 9-4, 19 Nov 63, 7°53′N 13°58′W, 50 m; 1 spec. 119 mm SL, Thierry 5, 31 Mar 64, 5°13′N 4°56′E, 70 m. Other West African — 3 spec. 237-242 mm SL, Walther Herwig 143/164, 20°31′N 17°42′W, 200 m (ISH); 1 spec. 180 mm SL, Undaunted 68-262, 24 Mar 68, 17°02′S 11°40′E, 55 m, 40′ trawl (TABL). Caribbean — 1 spec. 88 mm SL, 31 July 67, 10°53.5′N 61°00.6′W, 32-38 m; 1 spec. 162 mm SL, 7 Apr 68, 10°51′N 64°11′W, 33 m (MHNC).

ACKNOWLEDGMENTS

The bulk of the specimens used in this study were made available by William J. Richards, then at the Bureau of Commercial Fisheries Biological Laboratory, Washington; Bruce B. Collette, Bureau of Commercial Fisheries Ichthyological Laboratory, Washington; and Leslie W. Knapp, Smithsonian Oceanographic Sorting Center, Washington. Gerhard Krefft, Institut für Seefischerei, Hamburg, provided the "Walther Herwig" specimens. C. Godfrey Day provided unpublished data on drift bottles in the tropical Atlantic. Michael H. Horn and James E. Craddock have kindly read the manuscript. Financial support came from National Science Foundation grant GB-7108 to the Woods Hole Oceanographic Institution.

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CAMBRIDGE, MASS. 15 JANUARY, 1970 NUMBER 341

FOUR NEW SPECIES OF ELEPHANTIDAE FROM THE PLIO-PLEISTOCENE OF NORTHWESTERN KENYA

Vincent J. Maglio

ABSTRACT. Four new species and one new genus of fossil elephants are described from the Plio-Pleistocene of northwestern Kenya. *Stegotetrabelodon orbus* sp. nov. is more progressive and elephantinelike than its north African relative, *S. syrticus*, but it could not have been ancestral to the earliest Elephantinae. *Stegotetrabelodon* is placed in the family Elephantidae as a distinct subfamily, the Stegotetrabelodontinae. *Primelephas gomphotheroides* gen. et sp. nov. is described as the earliest known genus of the Elephantinae; it is morphologically and stratigraphically suitable as the basal genus from which later elephants could have been derived. *Loxodonta adaurora* sp. nov. is distinguishable from *Mammuthus africanavus*, in skull characters primarily, but also in dentition. It is considered to be the earliest known member of the *Loxodonta* lineage and may have been directly ancestral to the living *L. africana*. *Elephas ekorensis* sp. nov. is clearly related to, but is more primitive than, *E. recki* in both molar and skull morphology and is placed at the base of that lineage.

INTRODUCTION

In 1965, while working in Miocene deposits in Turkana District, northwestern Kenya, an expedition of the Museum of Comparative Zoology, under the direction of Professor Bryan Patterson, discovered fossil-bearing sediments of Plio-Pleistocene age well exposed in the drainage of the Kanapoi, a dry wash tributary to the Kakurio river (Patterson, 1966). The locality is at 36° 04′ E and 2° 19′ N, 38 miles west and 9 miles south of Teleki's volcano at the southern end of Lake Rudolf (Fig. 1). Clastic sediments predominate with pyroclastics interbedded throughout the sequence. The total measured thickness is over 200 feet but the vertical distribution of fossils indicates no major faunal change, though some new elements appear near the top of the section. Potassium/Argon age determinations of 2.9 ± 0.3 (Patterson, 1966), 2.7 ± 0.2 (Patterson *et al.*, in MS), and 2.5 ± 0.2 million years (Patterson and Howells, 1967) from an overlying basalt are questionable on

faunal evidence. Correlation based on Proboscidea (Maglio, in press) and Suidae (H.B.S. Cooke, pers. comm.) indicate near contemporaniety with Yellow Sands (Mursi Formation) at the base of the Omo sequence, for which the K/Ar date of 4.05 ± 0.2 million years is available (Howell, 1968).

The Kanapoi fauna is rich in vertebrate remains that include: cf. *Australopithecus* (Patterson and Howells, 1967); *Parapapio jonesi* (Patterson, 1968); *Lepus* sp.; *Hystrix* sp.; *Tatera* sp.; *Enhydriodon* sp. nov. (Kurtén, pers. comm.); *Hyaena namaquensis; Deinotherium bozasi; Anancus* sp.; *Loxodonta adaurora* sp. nov. (this paper); *Elephas ekorensis* sp. nov. (this paper); *Stylohipparion* sp.; *Ceratotherium* sp.; *Nyanzachoerus*, (2) spp. nov.; *Notochoerus* cf. *capensis; N.* cf. *N. euilus* (suid identifications by H.B.S. Cooke); Hippopotamidae, sp. nov. (S. Coryndon, pers. comm.); *Okapia* sp.; *Giraffa* sp.; *Tragelaphus* sp.; other Bovidae; *Crocodylus* sp.; *Euthecodon* sp.; *Podocnemis* sp.; *Testudo* sp. cf. *T. ammon;* Trionichydae indet., (Chelonia identifications by R. C. Wood); numerous remains of fish and molluscs.

Overlying the Kanapoi basalt is a small area of poorly exposed sediment at Ekora from which some vertebrate remains have been recovered. The locality is at 36° 11′ E and 2° 31′ N, 17 miles NNE of Kanapoi. The Proboscidea are the best preserved and most numerous fossils from these sediments. The tentative faunal list includes: *Anancus* sp.; *Loxodonta adaurora* sp. nov.; *Elephas ekorensis* sp. nov.; *Simopithecus* sp. (Patterson, pers. comm.); and *Ceratotherium* sp.

While exploring for further outcrops of the Kanapoi beds in 1967, a museum expedition worked a richly fossiliferous, thick sequence of sediments at Lothagam Hill (Patterson *et al.*, in MS). The exposures cover about three square miles and are situated at 36° 04′ E and 2° 53′ N, some 40 miles north of Kanapoi and three miles southwest of the Kerio delta on the southwestern side of Lake Rudolf. Two fossiliferous levels of coarser, red, fluviatile or deltaic sediments are separated by fine-grained lake beds probably representing a significant interval of time. On faunal evidence the upper fluviatile beds correlate with those of Kanapoi, but the lower beds, of which up to 1500 feet are exposed, appear to be considerably earlier. Though a K/Ar date of 3.71 ± 0.23 million years has been obtained for a basaltic sill between the lower fluviatile and the fine upper lake beds (Patterson, pers. comm.), this may represent no more than an upper limit for the age of the entire sedimentary sequence in the Lothagam area. The actual age of the

lower fluviatile beds would appear to be closer to 5.0–5.5 million years on faunal grounds (Maglio, in press). The fauna has not yet been studied in detail, but it includes: *Australopithecus* sp. cf. *A. africanus* (Patterson and Howells, in preparation); *Macaca* sp.; Anomaluridae, nov.; Hyaenidae indet.; Felinae indet.; Machairodontinae indet.; *?Civettictis* sp.; Orycteropididae, gen. et sp. nov.

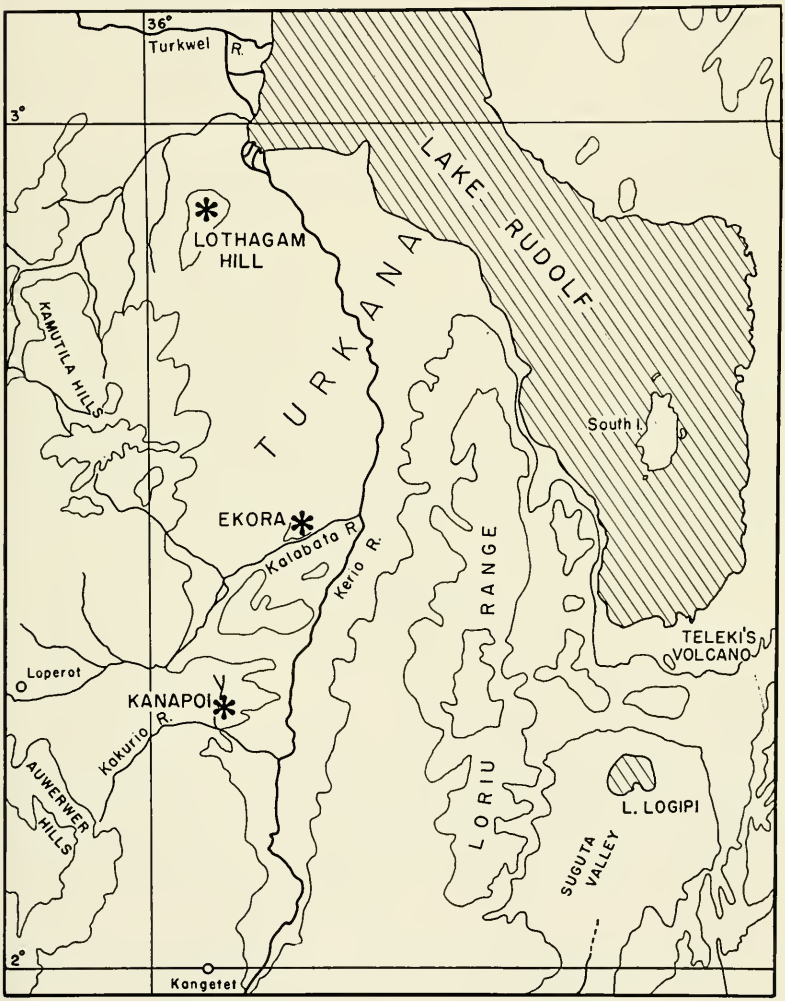

Figure 1. Generalized map of the southern Lake Rudolf area, northwestern Kenya, showing locations of the Kanapoi, Ekora and Lothagam deposits.

(Patterson, pers. comm.); *Deinotherium* sp.; Gomphotheriidae indet.; *Stegotetrabelodon orbus* sp. nov. (this paper); *Primelephas gomphotheroides* gen. et sp. nov. (this paper); *Stylohipparion* sp.; Rhinocerotidae, Brachypotherinae, nov.; *Nyanzachoerus,* (3) spp. nov. (Cooke, pers. comm.); Hippopotamidae, (2) spp. nov. (Coryndon, pers. comm.); *Giraffa* sp.; *Tragelaphus* cf. *T. nakuae; Gazella* sp.; *Redunca* aff. *ancystrocera;* other Bovidae (bovid identifications by A. W. Gentry); *Crocodylus* sp.; *Euthecodon* sp.; *Podocnemis,* (2) spp. nov. (R. C. Wood, pers. comm.); *Testudo* sp. cf. *T. ammon;* Trionychidae indet.; Squamata indet.; Pythoninae indet.; fish and mollusc remains.

Lothagam, Kanapoi, and Ekora have yielded numerous remains of Proboscidea of the families Gomphotheriidae and Elephantidae. Four new taxa of the latter group are represented in the collection and a detailed description of them is in preparation. Because of the importance of elephants for purposes of relative correlation, and because of the numerous, more fragmentary elephant remains turning up at other African localities, it seems desirable to present at this time a preliminary diagnosis of these new taxa to serve as a basis for comparison of less complete material. All specimens are at present in the Museum of Comparative Zoology but are the property of the National Museum, Nairobi. Specimen numbers given are catalogued in the National Museum, Centre for Prehistory and Palaeontology, Nairobi.

ELEPHANTIDAE
STEGOTETRABELODONTINAE *
Stegotetrabelodon Petrocchi 1941

Stegotetrabelodon, Petrocchi 1941:110.
Stegolophodon, Petrocchi, 1943:123.

Type Species. Stegotetrabelodon syrticus Petrocchi, 1941.

Emended Diagnosis. M3 with six to seven transverse plates superficially divided by vertical grooves; strong median cleft not extending to the base of the crown; complete enamel loops forming with moderate wear; prominent isolated accessory columns present

* Aguirre (1969) suggested that the genus *Stegotetrabelodon* ". . . may be a subfamily, Stegotetrabelodontinae . . . ," presumably of the Gomphotheriidae, though this is vague. However, no formal action to establish this subfamily was taken at that time. In this paper (and in press) I include this group as a subfamily of the Elephantidae.

behind the plates; crown height less than the width; enamel 4-7 mm in thickness, not folded; transverse valleys between plates open but V-shaped in longitudinal section; plates strongly triangular in longitudinal section; lamellar frequency, 2.5-3. Mandible with long, massive symphysis bearing very long incisors.

Distribution. Late Pliocene, Sahabi beds, Libya; lower fluviatile beds, Lothagam Hill, Kenya.

*Stegotetrabelodon orbus** sp. nov.
(Pls. I-II)

Type. PAL.LOTH. 354, complete left lower jaw with unworn left M_3, worn left M_2, and left and right lower incisor in situ, incomplete left and right M^3, complete right M^2 and skeletal fragments.

Horizon and Locality. Late Pliocene, lower fluviatile beds, Lothagam Hill, Kenya.

Hypodigm. Type and PAL.LOTH. 359, complete left and right M_3, left M^3 and right M^2 from a single individual. PAL.LOTH. 347, worn left M^3. PAL.LOTH. 349, complete right M_3. PAL. LOTH. 352, complete left M_3. PAL.LOTH. 355, partial left and right M_3. PAL.LOTH. 360, worn left M^3. PAL.LOTH. 367, complete right M^3. PAL.LOTH. 374, partial M^3 and skeletal fragments. PAL.LOTH. 342, complete left M_2 and partial right M_2. PAL.LOTH. 350, complete left and right M_2. PAL. LOTH. 366, complete left M^2. PAL.LOTH. 344, partial left dM^4 and dM_1. PAL.LOTH. 365, complete right dM_3.

Referred Material. PAL.LOTH. 368, left and right mandibular incisor and right premaxillary incisor. PAL.LOTH. 369, right humerus. PAL.LOTH. 370, right femur, left humerus, left and right fibulae and partial pelvis.

Diagnosis. About 12 per cent smaller than *S. syrticus*. Mandibular incisors short, forming about 38 per cent of the total jaw length. Free columns persisting only behind the first two plates on M3; relative crown height of M3 13 per cent greater than in *S. syrticus*. Lamellar formula:

$$\text{M3}\ \frac{6X,}{7X}\quad \text{M2}\ \frac{5X,}{6X}\quad \text{dM4}\ \frac{6,}{?}\quad \text{dM3}\ \frac{?}{3}$$

* L. *orbus*=childless. In allusion to the terminal position of this species and its apparent non-ancestry to later species of Elephantidae.

Discussion. In a series of papers, Petrocchi (1941, 1943, 1952, 1953) described a genus of Proboscidea, *Stegotetrabelodon,* from the late Pliocene beds of Sahabi, Libya. There can be little doubt as to the validity of this genus, but its significance as a morphological intermediate between the Gomphotheriidae and the Elephantidae has only recently been stressed (Aguirre, 1969; Maglio, in press). Petrocchi described two species of *Stegotetrabelodon, S. syrticus* and *S. "lybicus,"* and one of *Stegolophodon, S. "sahabianus,"* from the Sahabi beds. The latter two species were each based on a single molar. The type of *S. "lybicus"* is an unworn lower M3; comparison with the type mandible of *S. syrticus* is difficult owing to excessive wear in the latter. Nevertheless, the only differences between them are those expected to occur with wear. On present evidence the two must be considered conspecific. The type of *Stegolophodon "sahabianus"* is an incomplete M^3. Undoubtedly Petrocchi was struck by the progressive aspect of this specimen as compared with the lower molar of *S. "lybicus"* (the upper molars on the type skull of *S. syrticus* are severely worn). However, associated upper and lower molars of the new species from Lothagam described here show that the upper M3 was more progressive in structure than the lower, a common feature in Proboscidea generally. In size, the type molar of *S. "sahabianus"* is larger than the few known specimens of *Stegotetrabelodon* from Sahabi, but well within the expected range of size variation as exhibited for molars of the Lothagam species. Without more substantial evidence to the contrary, *Stegolophodon "sahabianus"* should also be considered as a synonym of *Stegotetrabelodon syrticus.*

The mandibular tusks of *S. syrticus* are about two-thirds as long as the premaxillary tusks. They are very long and slender, and form 57 per cent of the total jaw length in contrast to only 38 per cent for *S. orbus.* The type mandible of the latter is a young adult, however, and adult size of the mandibular incisors may have been proportionately somewhat greater. These tusks in *S. syrticus* are elliptical in cross-section, being compressed laterally. The lower tusks of *S. orbus* are also elliptical as are the small lower tusks of the dwarfed species, *Elephas celebensis* (Hooijer, 1954). The mandibular tusks of *S. syrticus* are nearly three times longer than in *S. orbus,* though similar in diameter.

The third molars are large and massive in *S. syrticus*; they are proportionately broader than in the Lothagam species (Table 1), but the crown height is about the same, resulting in a lower H/W

index (100 × height/width). A free column is present behind each molar plate in the Sahabi species, but in *S. orbus* all but the anterior two columns have become incorporated into the plates and are present in the form of small vertical ridges fused into the posterior faces of the plates. These may be absent on the more posterior plates. On molars of *S. syrticus,* a deep cleft divides the plates longitudinally; weaker, but still strong lateral clefts are present so that the apex of each plate is divided into four rather widely separated digitations that fuse with wear. In *S. orbus,* the lateral clefts are very weak and shallow, and all clefts are tightly compressed. Some of the apical digitations tend to be further subdivided into two or more smaller units, each separated by a weak cleft. The crown apex may thus have up to six or seven subdivisions. Upper molars of *S. orbus* are more progressive than the lowers in that the plates are more consolidated, with a weaker median cleft. There are seven plates on the lower and six on the upper M3 in both the Sahabi and the Lothagam species.

The second and first true molars of *S. orbus* are somewhat more progressive in appearance than M3. The plates are more consolidated, and apical digitations are separated only by weak and compressed clefts. The deeper median cleft perisits on the anterior two or three plates until intermediate stages of wear, but a complete enamel figure is formed on the remaining plates in early wear.

The enamel is very thick and smooth. Cement is abundant, but it usually does not fill the valleys completely nor does it usually invest the apex and sides of the molar plates.

The mandible is long anteroposteriorly in both species, but in *S. syrticus* the symphysis is 70 per cent longer than in *S. orbus,* though there is no difference in symphyseal width. Proximal tusk separation is nearly twice as great in *S. syrticus* as in the Lothagam species.

The systematic position of *Stegotetrabelodon* is clearly transitional between the Gomphotheriidae and the Elephantidae. Yet in spite of certain conspicuous gomphothere characters, such as long mandibular incisors and a prominent median cleft on M3, the molars are in general more elephant-like than gomphothere-like. In this genus, the inner and outer cones of the ancestral gomphothere molar are obliterated by median compression and fusion to form very platelike structures. The gomphothere trefoil pattern is gone and the old median folds that formed them persist as the free columns in the transverse valleys. Median swellings toward the base of the plates are all that remain of the anterior trefoil, whereas

the posterior one first became a prominent isolated column, and in the more advanced Elephantinae was fused into the plate face. These fused columns are responsible for the development of median "sinuses" on the wear figures of many elephant molars. *Stegotetrabelodon* is best placed in the family Elephantidae as a primitive subfamily.

With respect to reduction of mandibular incisors, increased relative crown height, fusion of isolated columns into the molar plates, and reduced division of the crown through compression and shallowing of clefts between the apical digitations, *S. orbus* sp. nov. would appear to represent a more progressive species than *S. syrticus*. Though very close in many particulars to the earliest Elephantinae, *S. orbus* was probably not ancestral to any known species of elephant, and occurs in the same deposits as the earliest species of Elephantinae (see below).

ELEPHANTINAE

Primelephas† gen. nov.

Type Species. *Primelephas gomphotheroides* sp. nov.

Diagnosis. Molars very low crowned, the height being one-half to three-fourths of the width; the median cleft lacking, but strong grooves superficially dividing the plates into prominent columns; plates wear as complete enamel loops; plates triangular in longitudinal section, wider toward the root; transverse valleys open to the base, but strongly V-shaped in cross-section; enamel 3-6 mm in thickness, not folded; lamellar frequency, 3-4. Cement abundant but usually not filling valleys completely. Mandible with very small but prominent incisors in some individuals, possibly males only; symphysis short. Lamellar formula:

$$M3\ \frac{7X}{8X},\quad M2\ \frac{5X}{6},\quad M1\ \frac{?}{5X}.$$

Distribution. Late Pliocene, lower fluviatile beds, Lothagam Hill, Kenya; Kolinga and ?Koulà, Tchad; Nyawiega, Kaiso beds, Uganda.

Included Species. *Stegodon korotorensis* Coppens, 1965.

Discussion. This genus is distinguished from the more primitive *Stegotetrabelodon* in having much reduced mandibular incisors and a short symphysis. The molars are elephantine in structure, lacking median clefts and having stronger plate development. In later

†L. *primus* = first, and L. *elephas* = elephant.

TABLE 1

Comparative measurements of *Stegotetrabelodon orbus* sp. nov. and *S. syrticus* for M3 and the mandibular incisors, in mm.

	Stegotetrabelodon orbus sp. nov.		*Stegotetrabelodon syrticus*	
	M_3	M^3	M_3	M^3
Length	234.3–280.3	212.1–255.9	280.0–317.4	232.0–242.0
Enamel thickness	5.0–6.9	4.0–7.4	5.5–6.0	5.3–7.2
Lamellar frequency	2.7–2.9	2.4–3.0	2.6–2.9	2.8–3.2
No. of plates	7X	6X	7X	6X
Maximum width	98.0–109.3	93.4–110.5	115.0–123.4	109.8–122.0
Maximum height	75.1–81.6	69.8–75.1	74.1	73.0–80.1
H/W index	69–87	68–75	60	66–67

Symphyseal length	513.2	869.6
Incisor length (exposed)	602.0	1671.0
Horizontal diameter	53.6	72.0
Vertical diameter	62.5	89.8
Proximal separation	18.2	29.5

genera of Elephantinae, the mandibular incisors disappear externally though they were probably present as tooth buds in symphyseal crypts in the early species of *Loxodonta* and *Elephas* (see below). In one case, mandibular incisors reappeared, possibly through paedomorphosis, in the dwarfed species *Elephas celebensis* Hooijer. The crown height is lower than in the most primitive species of later genera, and the number of plates is lower also. This genus appears structurally and chronologically to have been a member of the basal group from which later Elephantinae were derived.

In later genera the crown height is greater and the plates are not strongly triangular in longitudinal section; the anterior and posterior faces of each plate are nearly parallel. The transverse valleys between plates are broadly open and U-shaped, and the enamel is considerably thinner. In all but the most primitive known species of *Mammuthus,* the number of plates for each molar is greater than in *Primelephas.*

*Primelephas gomphotheroides** sp. nov.
(Pls. III-IV)

Type. PAL.LOTH. 351, associated left and right M^3, left M_3 and fragmentary palate.

Horizon and Locality. Late Pliocene, lower fluviatile beds, Lothagam Hill, Kenya.

Hypodigm. Type and PAL.LOTH. 358, left and right M^2, right M_2, left and right M_1, and mandibular symphysis. PAL.LOTH. 363, partial right M^3 and mandibular symphysis. PAL.LOTH. 375, incomplete right M_1.

Referred Material. PAL.LOTH. 364, fragmentary M_3. PAL. LOTH. 371, molar fragments, calcaneum, astragalus, incomplete fibula and an occipital condyle. PAL.LOTH. 376, molar plate.

Diagnosis. Lower crowned than *P. korotorensis* (Coppens), crown height for M3 60-65 per cent of crown width at base. Other characters as for the genus.

Discussion. Until recently, the most primitive known species of the Elephantinae was *Mammuthus subplanifrons,* a poorly known species from the older gravels of the Vaal River of South Africa, Kanam, and the Chemeron beds in east Africa, and the Chiwondo beds in Malawi (see Maglio, in press). Available data suggest that this species occurred in Africa earlier than the first

* *gomphotheroides* = gomphothere-like.

appearances of elephants in Europe and Asia (*M. meridionalis* and *E. planifrons* respectively), and it has been considered close to the ancestral stock of all later elephants. Recent study (Maglio, in press, and in preparation) has shown that *subplanifrons* is on the *Mammuthus* lineage and therefore did not occupy the more broadly ancestral position once allocated to it.

The stratigraphic position of *Primelephas gomphotheroides* is lower in the Pliocene section of Africa than is *M. subplanifrons,* or in fact any other known member of this subfamily. Morphologically, it is generalized enough to have served as the basis for later specializations that were to characterize the three later genera of elephants (*Elephas, Loxodonta,* and *Mammuthus*). The molars of *P. gomphotheroides* have a strong vertical ridge near the center of the plate faces, except on the first or second plates where the vertical ridges are free and columnar at their apices. With wear, these ridges form the median loops or sinuses so typical of early elephants. The number of plates is fewer and their relative height lower than in any other species of Elephantinae (Table 2). The enamel is thick and unfolded as in other early species. Transverse valleys between the molar plates are V-shaped in longitudinal section, but not compressed at the base as in the stegodonts. In all later species, including *M. subplanifrons,* the valleys are broadly open and U-shaped at the base; this serves to maintain the efficiency of the tooth as a grinding surface into late stages of wear by keeping the enamel ridges separated by a cement interval down to the base of the crown.

The symphysis of the jaw is much shorter than in *Stegotetrabelodon,* even though small incisors are present. As a result, the root of the incisor passes into the horizontal ramus. These incisors are no longer closely appressed in the midline of the symphysis as in *Stegotetrabelodon,* but lie on either side of the "spout" formed by the downturned symphysis. They extend along the ventral wall of the horizontal ramus anterior and somewhat beneath the front portion of the mandibular canal. There is some indication of variation in size for these incisors; in two very fragmentary mandibles there apparently were no external tusks but only a pair of deep cavities lateral to the symphysis and connected to the mandibular canal by a short channel. These two specimens may represent juvenile individuals, but it is also possible that incisor size or even their presence or absence was a sexual character, being larger in the males.

Specimens referable or probably referable to *Primelephas* are known from other African localities. Several molar fragments

from Nyawiega in the Kaiso sequence indicate the presence of a closely related form. Although tentatively referring this material to *M. subplanifrons* (Cooke and Coryndon, in press), H. B. S. Cooke independently recognized the primitive nature and generic distinctness of some of the specimens, but was unable to diagnose this new form without better material. All of the Kaiso material referred by Cooke and Coryndon to *M. subplanifrons* is the same and should be referred to *Primelephas*. Although additional data may show this form to be specifically distinct, on present evidence it is best referred to *Primelphas gomphotheroides*.

A small fragment was described by Coppens (1965) from Tchad as *Stegodon korotorensis* sp. nov. This specimen is very incomplete, consisting of the posterior three plates of a lower M3, but it is clearly not a true *Stegodon*. The plates are divided apically into only a few well-separated digitations, and, though V-shaped in longitudinal section, the transverse valleys are not compressed at the base as they are in stegodonts. The only other known specimen, an equally incomplete upper M3, is similar to the type. This form is very close to the Lothagam and Kaiso specimens and should be included in the genus *Primelephas*. These two specimens of *P. korotorensis* are distinguishable from *P. gomphotheroides* in being proportionately higher crowned, but otherwise they are too fragmentary for diagnosis of the species, and more detailed comparisons with material from other localities is not possible. On present evidence we must recognize two species of *Primelephas*—*P. gomphotheroides* and *P. korotorensis*.

Loxodonta F. Cuvier 1825

Type Species. *Loxodonta africana* (Blumenbach) 1797.

Loxodonta adaurora† sp. nov.

(Pls. V-VI)

Elephas cf. *meridionalis* Nesti, MacInnes, 1942: 92.
Archidiskodon exoptatus Dietrich (in part), Dietrich, 1942: 72.††

†L. *adaurora*=at dawn.

††In a review of the syntype collection of *"Archidiskodon exoptatus,"* I (1969) have shown that two distinct taxa are present—one is referred to *Elephas recki* Dietrich 1916, and is represented by the better specimens in the collection; the other taxon is a more primitive species. The specimens of the latter taxon are insufficient for the establishment of a species and a *recki* specimen was chosen as the lectotype of *"A. exoptatus."* The non-*recki* material in the syntype collection from Lactolil is here referred to *L. adaurora* sp. nov.

TABLE 2

Comparative measurements in mm for M3 of *Primelephas gomphotheroides* gen. et sp. nov. from Lothagam Hill with specimens from other African localities. Superscripts "e" indicate an estimated value.

	Primelephas gomphotheroides gen. et sp. nov.				*P. korotorensis*	
	LOTHAGAM		KAISO		TCHAD	
	M_2	M^3	M_2	M^3	M_2	M^3
Length	247.5	208.1	—	—	—	—
Enamel thickness	3.5–5.1	3.4–5.6	4.0–4.9	—	4.0–4.5	5.0–6.0
Lamellar frequency	3.3	3.2	3.6	—	3.8	3.4
No. of plates	8X	7X	—	—	—	—
Width	93.2	93.9–94.3	109.5	89.2	86.3	85.0[e]
Height	61.2	59.5–60.1	52.1	52.8	65.0[e]	60.0+
H/W index	65	63–64	57	59	72[e]	76[e]

Elephas cf. *planifrons* Falconer and Cautley, Arambourg, 1947: 114. *"Elephas . . . close to E. exoptatus"*, Patterson, 1966: 5.

Type. PAL.KANAP. 385, a nearly complete skeleton, the skull and jaws bearing partially worn last molars in situ.

Horizon and Locality. Plio-Pleistocene, Kanapoi beds, Kenya.

Hypodigm. Type and PAL.LOTH. 353, skull with left M^2-M^3, right M^3 and left premaxillary incisor. PAL.KANAP. 383, left and right M^3, worn left M^3 and incomplete left and right M_3. PAL.KANAP. 390, complete right M^3. PAL.KANAP. 407, complete right M_3. PAL.EKA. 423, palate with left and right M^3. PAL.KANAP. 386, left M^2. PAL.KANAP. 389, incomplete right M^2. PAL.KANAP. 403, partial ramus with incomplete left M_2. PAL.KANAP. 406, jaw ramus with r.M_1-M_2. PAL.KANAP. 381, jaw with left and right M_1. PAL.KANAP. 391, right dM^4. PAL.KANAP. 411, right dM^4, left and right dM_3. PAL.KANAP. 382, right dM^3. PAL.KANAP. 396, right dM^3. PAL.KANAP. 392, right dM^2. PAL.KANAP. 400, left dM_2.

Localities for Hypodigm. All from the Kanapoi beds except 353, which is from the upper fluviatile beds at Lothagam Hill, and 423, from Ekora.

Diagnosis. Molars low crowned, the height equal to or less than the width; enamel thickness 3-5 mm and not folded; very large anterior and posterior enamel folds forming prominent loops or sinuses with wear. Plates thick and well separated, the lamellar frequency being about 2.5-4. Lateral sides of plates lacking the strong tapering as in *M. africanavus.* Skull like that of *L. africana* but with very large and somewhat flaring premaxillae, long frontal, and prominent fronto-parietal ridges lateral to external naris. Parietals and occipitals not expanded. Occipital condyles high and projecting. Tusks long and gently curved in a single plane, not twisted as in *Mammuthus.* Mandible with vestigial incisive cavities. Lamellar formula:

M3	M2	M1	dM4	dM3	dM2
8-10, / 10-11	7, / ?	? / 6	5, / ?	5, / 5	3. / 3

Discussion. Until now there has been little direct evidence concerning the early stages in the evolution of *Loxodonta africana.* Coppens (1965) placed the north African species *Mammuthus africanavus* on the *Loxodonta* lineage, but recent study and new material (Arambourg, pers. comm.) show that *africanavus* was not on that line.

Other early elephants such as *Elephas planifrons* from the Villafranchian of Asia, and *M. meridionalis* from deposits of similar age in Europe, were already differentiated along different lines and were unrelated to the living African elephant. The African Plio-Pleistocene species, *M. subplanifrons,* though poorly known, has *Mammuthus* affinities and also appears to have been unrelated to *Loxodonta.* From all available evidence, *Loxodonta adaurora* sp. nov. is the only known species certainly on the *Loxodonta* lineage, and extends this line back to the earliest Pleistocene or latest Pliocene in Africa.

The earliest known representatives of the three Pleistocene genera of Elephantinae, *Loxodonta, Mammuthus,* and *Elephas,* were not yet greatly differentiated with respect to dentition, though distinct on skull characters. This fact has resulted in the confusion of these lines when only teeth were available for study. In *L. adaurora, M. africanavus,* and *E. planifrons,* the molars are all rather low crowned, being about as high as they are wide; the enamel is thick and unfolded with a more or less prominent median fold or loop caused by the partial fusion of intravalley columns into the face of the plates; and the number of plates is similar, about 9-12 for M3 (Table 3). Nevertheless, certain differences occur in the molars that distinguish populations of these three species. In *M. africanavus* the sides of the plates taper strongly toward the apex of the crown, and the molar tends to be proportionately narrower than in either *L. adaurora* or *E. planifrons.* The lamellar frequency for *M. africanavus* is somewhat greater than for *L. adaurora,* the latter being more primitive in this respect. Finally, the relative crown height for M3 of *africanavus* is nearly 20 per cent greater than for *L. adaurora.* The lamellar frequency, crown height, and other parameters for the known specimens of *E. planifrons* from the Siwalik Hills show a considerably greater degree of variation than for other well known species. Yet there exists every intermediate stage between the extremes for each measurable parameter. It seems likely that in *E. planifrons* we are dealing with an evolutionary series of populations for which stratigraphic control is lacking.

Far more important for the determination of generic criteria in these early elephants are the skulls (Figs. 2 and 3), which are very different in the three lines and clearly establish relationships with later species. The cranial morphology for *L. adaurora* and *E. planifrons* are each known from several specimens. The skull of *M. subplanifrons* is unknown and that of *M. africanavus* is known

only from a poorly preserved referred skull recently described by Professor Arambourg. Though this description is not yet published, photographs kindly supplied by Professor Arambourg show that this species is on the *Mammuthus* line and that it was close to, but

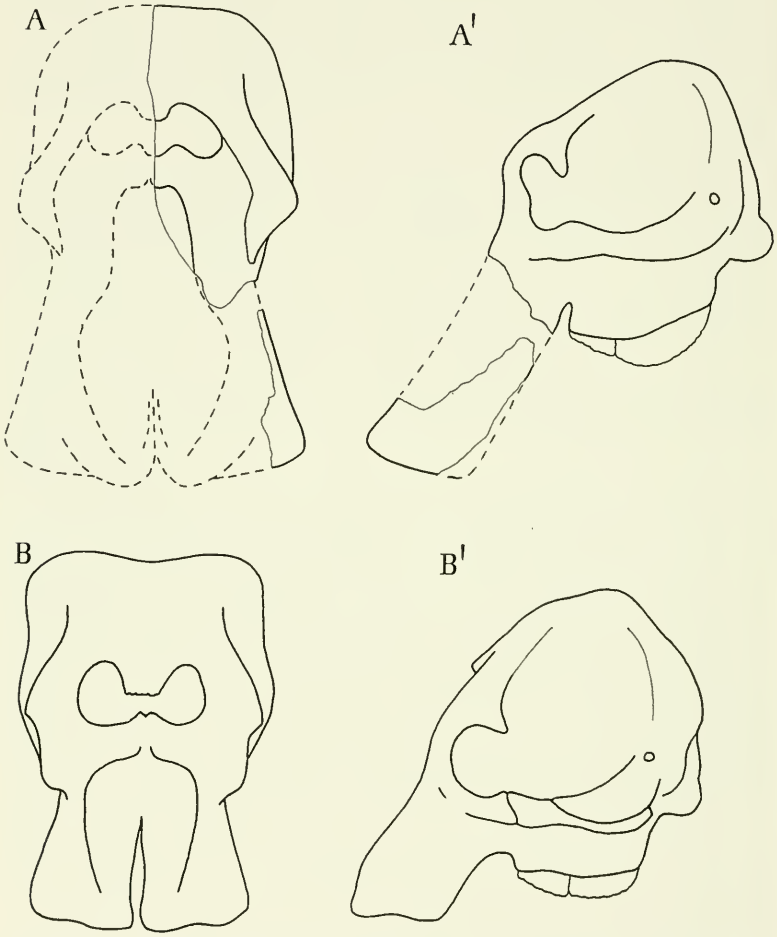

Figure 2. Diagrammatic representation of skull shape for two species of *Loxodonta*. A, *Loxodonta adaurora* sp. nov. B, *Loxodonta africana*. For each: left, anterior view; right, left-lateral view. A is based on PAL. LOTH. 353 (solid line) and PAL.KANAP. 385 (broken line). Not to scale.

more primitive than, *M. meridionalis*. The following cranial comparisons are made with the later species representing the *Mammuthus* type.

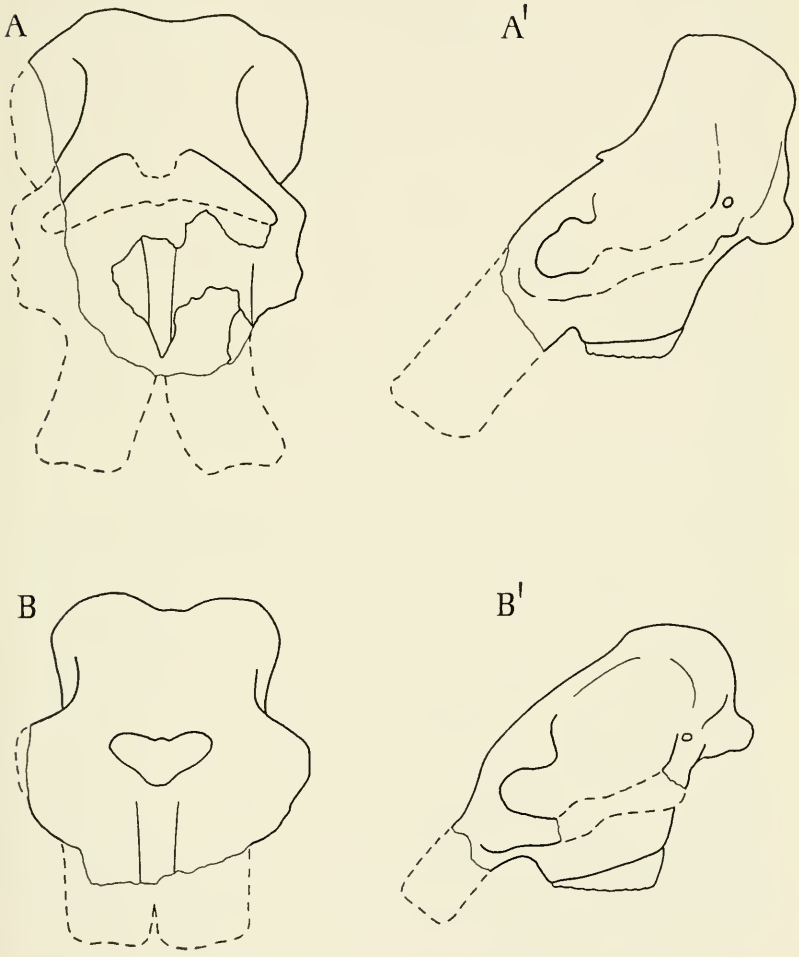

Figure 3. Diagrammatic representation of skull shape for early species of *Mammuthus* and *Elephas*. A, *Mammuthus meridionalis*. B, *Elephas planifrons*. For each: left, anterior view; right, left-lateral view. Reconstructions based on several specimens: A, Geol. Inst., Univ. of Florence Nos. 1049, 1051 and 1054. B, British Museum (N.H.) No. 3060 and Panjab Univ. specimen, no number.

Elephas planifrons, (Fig. 3B).

Although tusks are lacking from the four known skulls of this species, isolated incisors probably referable to it from the Siwalik Hills and an associated tusk with *planifrons* dentition from Bethlehem (Hooijer, 1958) indicate that the tusks were gently curved in a single plane, and probably not very large. The fronto-parietal surface is flat and broad, and separated laterally from the temporal fossa by a sharp ridge formed where the parietal bone makes an acute angle between the two surfaces. This ridge is more sharply defined in later species of *Elephas,* and in the living species it is very prominent along the lateral margins of the forehead. The parietals and occipitals are slightly expanded with a median-sagittal depression typical of this genus. The temporal constriction is slight, resulting in a very broad fronto-parietal surface. The occipital condyles are situated high on the head, about one-third down from the dorsal surface of the occiput. The external naris is very small and not downturned at the sides. The tusk sockets appear to have been moderately separated and the premaxillae are nearly parallel to the fronto-parietal plane. The latter is inclined at about 55 to 60 degrees to the vertical axis of the skull measured perpendicular to the palate. As a result, the tusks are directed forward and downward. The skull is greatly compressed parallel to the facial axis.

Mammuthus meridionalis. (Fig. 3A).

The tusks in *Mammuthus* are typically massive and spirally twisted. The tusks on the skull of *M. africanavus* (Arambourg, pers. comm.) and a tusk associated with a molar of *M. subplanifrons* (Meiring, 1955), have this structure. The fronto-parietal surface is strongly concave dorsoventrally and flat to slightly convex in the lateral direction. A prominent but rounded angle of the parietal separates the fronto-parietal surface from the temporal fossa. The parietals and occipitals are expanded dorsally so that the occipital condyles lie closer to the level of the palate than to the top of the occiput. The external naris is large and laterally elongated; it is slightly downturned at the sides. The tusk sockets are closely spaced proximally, but diverge distally. The premaxillae are nearly parallel to the fronto-parietal plane, and the latter forms an angle of about 50 to 55 degrees with the vertical axis of the skull. As in *E. planifrons,* the tusks are directed forward and downward. As in *Elephas,* the skull is strongly compressed parallel to the facial axis.

Loxodonta adaurora sp. nov. (Fig. 2A)

The tusks are massive, but only gently curved upward, and are in a single plane. As in *L. africana,* the fronto-parietal surface is slightly convex in both the dorsoventral and lateral directions, but the frontal is proportionately longer, resembling *Elephas* more in this respect. As a result, the orbits are lower on the head than in *L. africana.* The forehead curves laterally into the temporal fossae without a sharp, angular border. The parietals are not expanded, nor is the occipital region which, like the living African species, is nearly flat posteriorly. The highest point of

the parietals is in the mid-sagittal line; there is no median depression. The temporal constriction is very slight, as in the recent species. The occipital condyles are low on the skull. The external naris is large and weakly downturned at the sides. Tusk sockets are widely separated and flaring distally; these are far more massive than in the living species. The premaxillae and maxillae are fused in the median line for their entire length and form an angle of about 20 degrees to the fronto-parietal plane. In *L. africana* this angle is about 15-20 degrees. The fronto-parietal plane is inclined at about 45 degrees to the vertical axis of the skull, and is therefore more nearly vertical in orientation than in *E. planifrons* or *M. meridionalis.* The skull is only slightly foreshortened in the anteroposterior direction and the skull is more nearly rounded in shape than it is in either *Mammuthus* or *Elephas.*

In *Loxodonta adaurora,* a pair of elongated cavities near the symphysis suggests the presence of vestigial incisive buds, but these apparently never developed into external tusks. These cavities communicate posteriorly with the mandibular canal by a narrow channel. Such structures have also been observed in two mandibles of *E. planifrons* in the Indian Museum. In those early elephants with external mandibular tusks, such as *E. celebensis* and *P. gomphotheroides,* a narrow channel passes forward from the anterior end of the mandibular canal into the enlarged alveolus for the incisor. Vestigial incisive cavities have not been observed in more progressive fossil species or in the two living species.

Despite the numerous references to *E. planifrons* in Africa (e.g. Joleaud, 1928; Romer, 1928; Kent, 1941; MacInnes, 1942; Arambourg, 1947, 1948a, and 1948b, etc.), that species does not appear to have occurred outside of Asia.* Specimens so referred in Africa probably belong either to *M. africanavus* or to *L. adaurora.* The former appears to have been confined to north Africa, but the data are inconclusive. Material probably referable to *L. adaurora* has been recovered from the Kaiso formation (Cooke and Coryndon, in press), Kanam, Yellow Sands (Omo), Laetolil (Maglio, 1969), the Chemeron beds, and the Chiwondo beds (Mawby, in preparation). (See appendix for a discussion of specimens from the Vaal River).

Morphologically, *L. adaurora* is distinct from *M. africanavus,* with which it is often confused on molar evidence alone. It appears to have been the dominant elephant during the late Pliocene and

* Specimens called *E. planifrons* from Europe belong to early stages of *M. meridionalis.*

early Pleistocene of east Africa but was quickly replaced by *Elephas recki,* which became the dominant species until middle Pleistocene times.

All evidence indicates a close relationship between *L. adaurora* and *Primelephas gomphotheroides.* Thus, *Loxodonta* appears to have differentiated very early in the history of the subfamily.

Elephas Linnaeus 1758

Type Species. Elephas maximus Linnaeus 1758.

*Elephas ekorensis** sp. nov.

(Pl. VII)

Type. PAL.EKA. 424, left and right M^3.

Horizon and Locality. Plio-Pleistocene, Ekora beds, Ekora, Kenya.

Hypodigm. Type and PAL.KANAP. 387, partial right M^3 and right M^2. PAL.KANAP. 395, partial left M^3. PAL.EKA. 420, mandible with incomplete left M_2. PAL.KANAP. 412, incomplete right M^2.

Referred Material. PAL.EKA. 422, skull with eroded palate, lacking teeth.

Localities for Hypodigm. 420 and 422 from the type locality; 395, 387 and 412 from the top of the Kanapoi beds.

Diagnosis. Molars with crown height 10-25 per cent greater than width; M3 broader anteriorly, becoming very narrow posteriorly; anterior and posterior sinuses very prominent; enamel 3-4 mm thick and very weakly folded near the bases of the plates. Plates well separated with a lamellar frequency of about 3.5-4. Eleven plates plus a strong heel on M^3. Skull compressed parallel to the fronto-parietal plane; parietals slightly expanded with a mid-sagittal depression; fronto-parietal surface strongly inclined to the vertical axis of the skull; external naris very large; strong fronto-parietal flanges forming a sharp angle between the forehead and temporal fossae; tusk sockets parallel, widely separated and parallel to the facial axis.

Discussion. The molars of *Elephas ekorensis* sp. nov. are clearly distinguishable from those of *Loxodonta adaurora,* with which they occur both in the upper part of Kanapoi and at Ekora. The plates in the former are thinner and more closely spaced, and the enamel is weakly folded on moderately worn plates. The

* *ekorensis* = the elephant from Ekora.

TABLE 3

Comparative measurements for M3 of *Loxodonta adaurora* sp. nov., *Mammuthus africanavus* and *Elephas planifrons*, in mm.

	Loxodonta adaurora sp. nov.		*Mammuthus africanavus*		*Elephas planifrons*	
	M^3	M_3	M^3	M_3	M^3	M_3
Length	228.1–302.2	277.1–305.1	?250–300	281.1–295.0	201.0–292.4	181.0–321.3
Enamel thickness	3.1–4.8	3.0–4.8	3.4–5.0	3.0–4.6	2.8–5.2	2.0–5.0
Lamellar frequency	2.5–3.9	2.9–3.9	3.0–4.9	3.6–4.9	2.6–5.5	3.3–5.8
No. of plates	8–10	10–11	9	10–11	9–12	9–13
Width	103.6–124.9	96.5–115.1	88.2–108.0	81.2–105.0	90.0–110.1	72.0–110.0
Height	90.4–109.2	90.1–103.0	84.1–103.2	97.9–114.3	83.0–129.0	75.0–116.0
H/W index	90–99	89–93	93–97	100–118	84–109	72–115

crown height is greater than the width and M3 narrows posteriorly, unlike that tooth in *L. adaurora*. The skulls of the two species are very different. In *E. ekorensis* (Fig. 4A), the premaxillae do not flare as in the Kanapoi species, the parietals are expanded laterally and dorsally with a median-sagittal depression as in *E. planifrons* (Fig. 4D), so that the brain case is widest in this region and not in the auditory region as in *L. adaurora*. The skull is compressed as in *E. planifrons* and *E. recki*, and contrasts with the more rounded skull of *L. adaurora*. The fronto-parietal axis of *E. ekorensis* is strongly inclined to the vertical axis of the skull, again in contrast to the condition in *Loxodonta*. The skull differs from that of *E. planifrons* in having more prominent, widely separated tusk sockets and a very large external naris.

As discussed elsewhere (Maglio, in press), the earliest recognizable stage of *E. recki* (stage 1 of 4 stages there recognized) occurs at Kikagati, Uganda. This form is close to *E. ekorensis*, but differs significantly in having proportionately thinner enamel, a greater lamellar frequency, and a proportionately higher crown. There also appears to have been a greater number of plates on M3. Abundant elephant remains, including skull material, from the White and Brown Sands localities at Omo probably represent stage 1 *recki*, but this material has not yet been studied in detail. The cranial remains are similar to the skulls of stage 2 *recki* described by Arambourg (1947) from the type Omo area (Coppens, pers. comm.), and in the following discussion comparisons of *E. ekorensis* are made with the latter material.

The skull of *E. ekorensis* differs from that of stage 2 *recki* (and probably stage 1 as well), though the differences are in degree only (Fig. 4A and B). The facial compression, expanded parietals, strong frontal flanges, parallel tusk sockets, and inclination of the facial axis to the vertical axis of the skull are characteristic features of the two species, but in *E. ekorensis* these are only weakly developed in comparison with *E. recki*. The fronto-parietal region in the Ekora species is still relatively flat; the anterior expansion of the parietals is not yet evident. In *recki*, the fronto-parietal area is concave anteroposteriorly because of the forward expansion of the parietal vault. The tusk sockets of *recki* are more closely spaced than in *E. ekorensis* and the external naris is larger and strongly downturned at the sides.

In both cranial and dental characteristics, *E. ekorensis* is considerably less progressive than *E. recki*. The Ekora sediments appear to be earlier than Tuff B at Omo, which is the earliest recorded occurrence of *E. recki*. An ancestral-descendent relationship between these two species is indicated by present evidence.

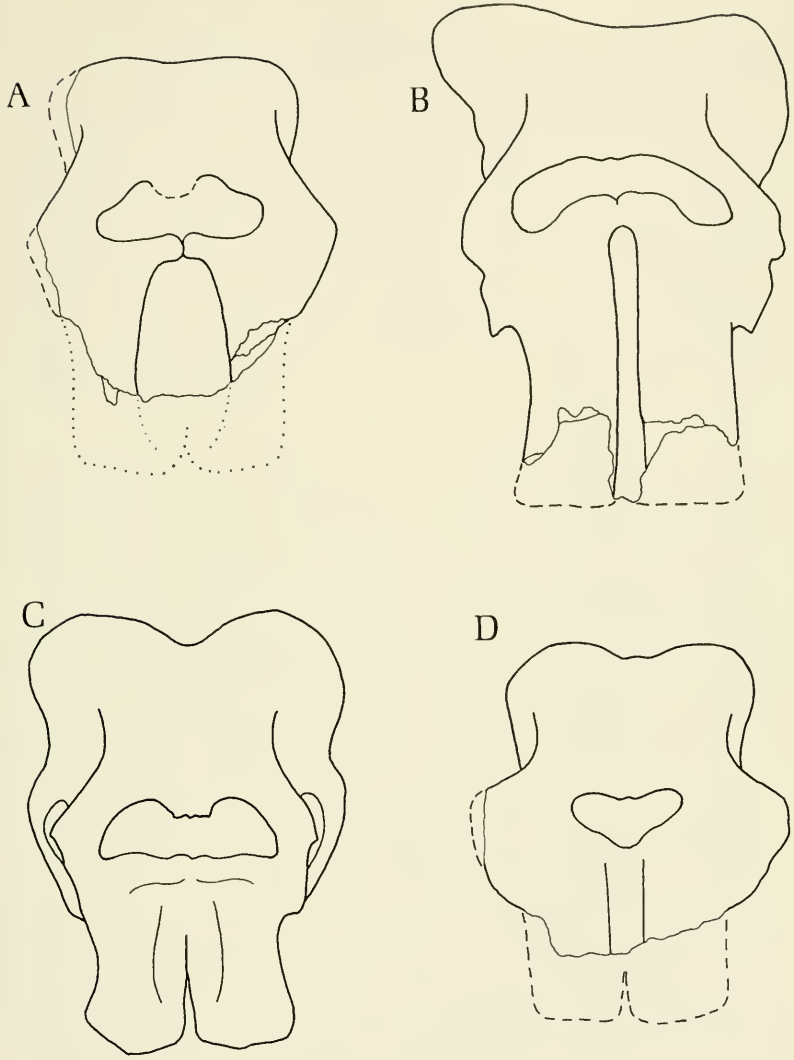

Figure 4. Diagrammatic comparison of skull shape for species of *Elephas*. A, *Elephas ekorensis* sp. nov. B, *Elephas recki*. C, *Elephas maximus*. D, *Elephas planifrons*. Anterior view. Reconstruction in dotted lines for A is conjectural. Not to scale.

TABLE 4

Comparative measurements for M3 for *Elephas ekorensis* sp. nov. and two early stages of *Elephas recki*, in mm.

	EKORA		KIKAGATI		OMO	
	Elephas ekorensis sp. nov.		*E. recki*, stage 1		*E. recki*, stage 2	
	M^3	M_3	M^3	M_3	M^3	M_3
Length	276.9–304.1	—	—	—	205.7–265.0	228.0
Enamel thickness	3.0–4.6	3.4–4.2	2.9–3.1	2.8–3.4	3.0–4.0	2.5–3.5
Lamellar frequency	3.3–3.9	3.8–4.2	4.2	4.7–5.0	5.0–5.8	5.0–5.9
No. of plates	11	—	—	12–13?	12–14	12–13
Width	94.9–96.6	72.7–80.2	86.6	80.1–85.5	81.4–92.9	59.5–83.0
Height	105.6–113.2	87.5–102.3	103.1	104.8–112.2	109.1–127.0	85.0–120.2
H/W index	111.4–117.2	115.8–127.7	119.0	126.6–133.0	123.8–151.1	136.0–153.0

CONCLUSIONS

The abundant new proboscidean material now available from the Plio-Pleistocene deposits at Lothagam, Kanapoi, and Ekora helps significantly to bridge previous gaps in our knowledge of the origin and early stages in the evolution of the Elephantidae. This material is all the more important because it allows a means of relative correlation based on elephants that has been shown to be of great potential value, even for poorly known localities (Maglio, in press). The transition from gomphothere to elephant now seems established, and the time and place of the origin of the Elephantidae is reasonably determined as the later Pliocene of Africa. Morphological evidence strongly favors a monophyletic origin for this group.

APPENDIX

A number of elephant species based on incomplete type specimens have long caused confusion in the literature because they are inadequate to provide the kind of diagnosis necessary for fossil species. The following described taxa may be conspecific with *Loxodonta adaurora* or possibly with *Mammuthus africanavus*, but should not be given priority because of inadequacy of the types which are, in most cases, the only known specimens. The localities are vague and the stratigraphic relationships are essentially unknown.

Archidiskodon vanalpheni Dart, 1929. A single incomplete left M^3 from the Middle Terrace of the Vaal River, South Africa. The stratigraphic relationships are uncertain, and it is not possible to determine the total number of plates with confidence, though there may have been about ten. The plates are broad and well separated; the specimen resembles M^3 of *L. adaurora*.

Archidiskodon milletti Dart, 1929. An incomplete left M^3 from the Middle Terrace of the Vaal River. The plates are somewhat thinner than in *A. vanalpheni*, but not significantly. As with that form, the specimen is insufficient for adequate comparison with other material, without skull evidence.

Archidiskodon loxodontoides Dart, 1929. A single fragmentary left M^3 from the Middle Terrace of the Vaal River. From what remains this specimen appears to be close to the previous two forms, but specific diagnosis is not possible.

Loxodonta griqua Houghton, 1922. Several very fragmentary specimens from the Vaal River gravels, horizon unknown. This material is too incomplete to allow confident specific comparison with any other specimen. It was made the type of a new genus, *Metarchidiskodon*, by Osborn (1934).

From all available evidence, the above material appears to be close to east African material here referred to *Loxodonta adaurora,* and to specimens of *M. africanavus,* but specific identity with either can not be proved because of the incomplete morphological and stratigraphic data. The South African specimens have a greater lateral taper to the plates than do those of *L. adaurora* and in this respect are closer to *M. africanavus.* The types are inadequate for specific diagnosis and in view of the excellent and complete material from other localities, they should not be used as the basis for specific comparison with material for which stratigraphic data and associated faunas are known.

The names *A. vanalpheni, A. milletti, A. loxodontoides,* and *L. griqua* must be considered *nomina dubia,* and the names applied only to the type specimens.

ACKNOWLEDGEMENTS

I am grateful to Professor Bryan Patterson for permission to study the proboscidean remains collected during expeditions of the Museum of Comparative Zoology. The fossil material was sent to Harvard University with the kind cooperation of the Ministry of Natural Resources of the Kenya Government and of the National Museum. Comparative material was made available through the courtesy of Dr. C. Arambourg, Museum of Natural History, Paris; Dr. F. Azzabi, Museo Libico di Storia Naturale, Tripoli; Dr. A. Berzi, Museo di Geologia e Paleontologia, Università di Firenze; Dr. D. A. Hooijer, Rijksmuseum of Natural History, Leiden; Mr. R. E. Leakey, National Museum, Nairobi; Dr. L. S. B. Leakey, Centre for Prehistory and Paleontology, Nairobi; Prof. J. P. Lehman, Museum of Natural History, Paris; Dr. R. Liversidge, McGregor Memorial Museum, Kimberley; Dr. K. H. Fischer, Institute for Paleontology, Humboldt University, East Berlin; Dr. I. C. Pande, Department of Geology, University of Chandigarh; Dr. Petronio, Department of Geology, Città Universitaria, Rome; Dr. M. V. S. Sastri, Indian Museum, Calcutta; Dr. A. Sutcliffe, British Museum (Natural History); and Dr. R. Tedford, The American Museum of Natural History. I have benefited greatly from discussions with Drs. E. Aguirre, C. Arambourg, H. B. S. Cooke, Y. Coppens, Mrs. S. Coryndon, and Dr. D. A. Hooijer. Prof. Bryan Patterson read the manuscript and offered helpful comments.

The field work and research was supported in part by grants from the National Geographic Society and the Museum of Comparative Zoology to the author, by NSF Grants no. GP-1188 and

GA-425 to Prof. Patterson, and by an Evolutionary Biology Training Grant to the Department of Biology, Harvard University, NSF Grant no. BG-7346 (Reed C. Rollins, principal investigator).

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PLATES

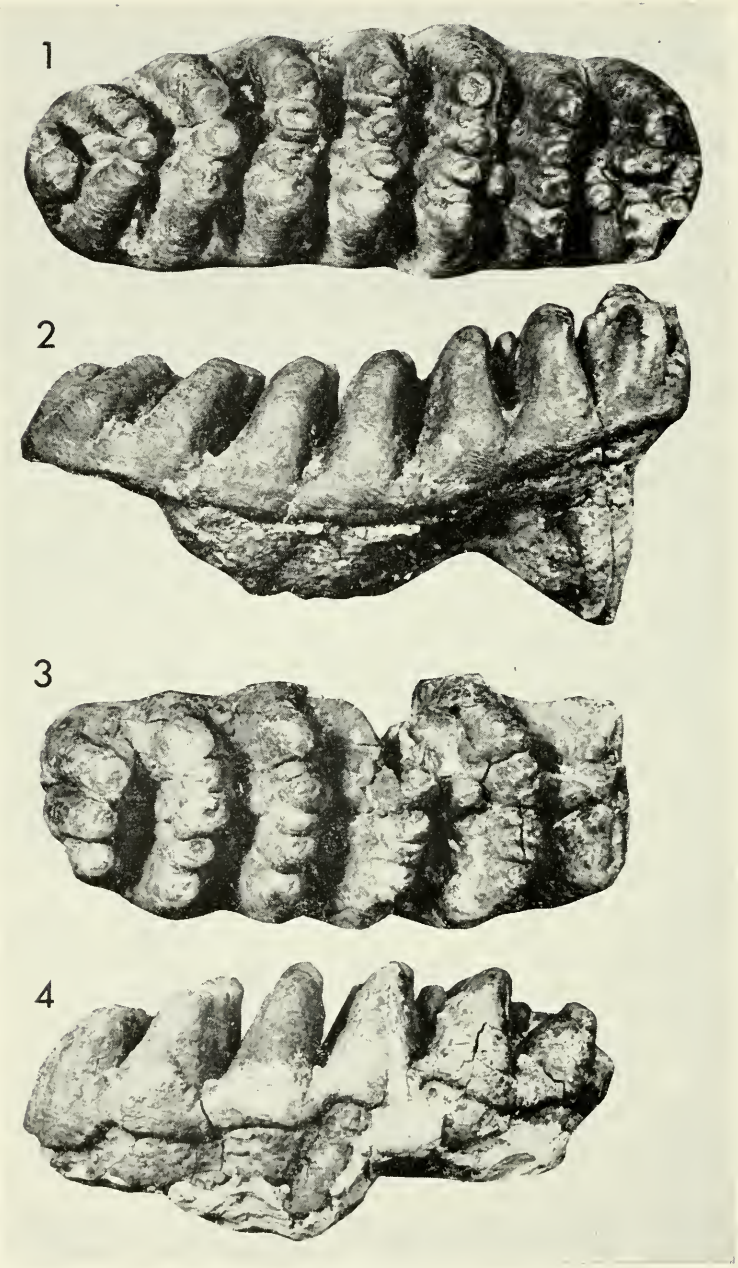

PLATE I

PLATE I

1. *Stegotetrabelodon orbus* sp. nov. PAL.LOTH. 359, r.$M_{\frac{2}{3}}$. Occlusal view. × ⅓.

2. *Stegotetrabelodon orbus* sp. nov. PAL.LOTH. 359, r.$M_{\frac{2}{3}}$. Buccal view. × ⅓.

3. *Stegotetrabelodon orbus* sp. nov. PAL.LOTH. 359, l.M^3. Occlusal view. × ⅓.

4. *Stegotetrabelodon orbus* sp. nov. PAL.LOTH. 359, l.M^3. Buccal view. × ⅓.

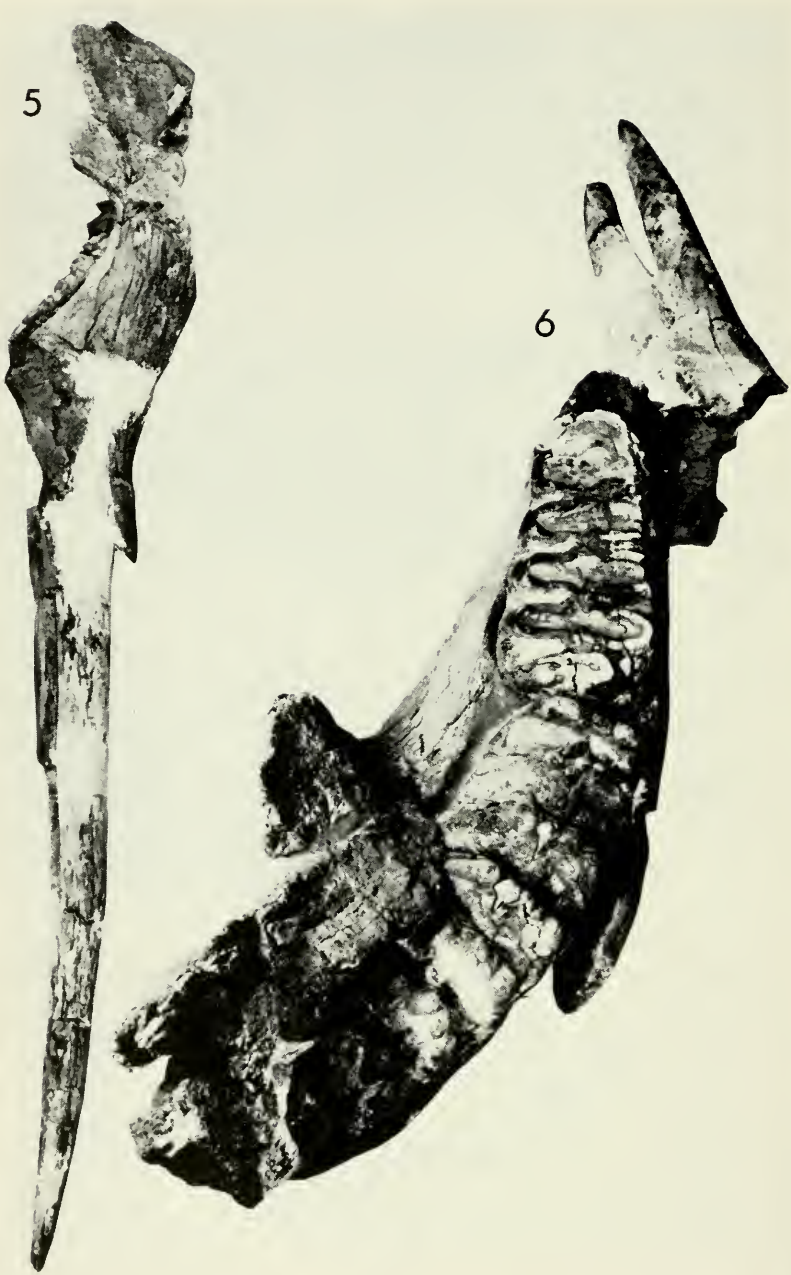

PLATE II

PLATE II

5. *Stegotetrabelodon orbus* sp. nov. Type. PAL.LOTH. 354, mandible with M_2-M_3. Left-lateral view. Approx. × 1/10.

6. *Stegotetrabelodon orbus* sp. nov. Type. PAL.LOTH. 354, mandible with M_2-M_3. Dorsal view. Approx. × ¼.

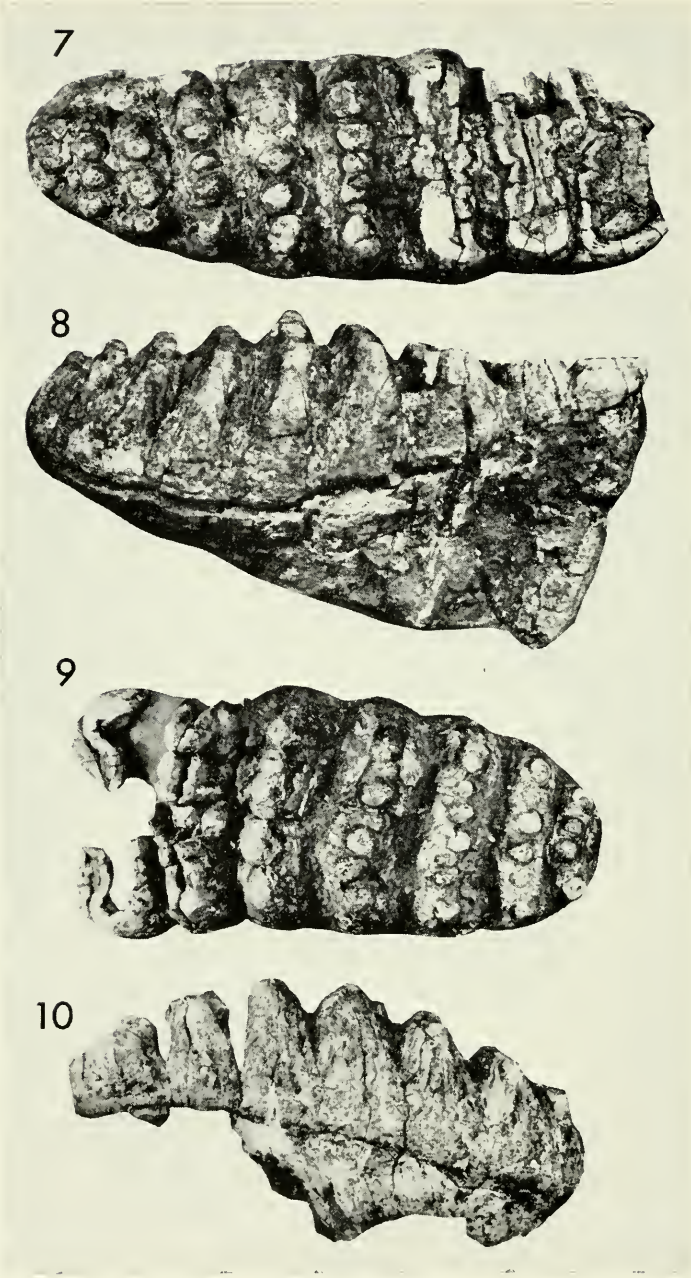

PLATE III

PLATE III

7. *Primelephas gomphotheroides* gen. et sp. nov. Type. PAL.LOTH. 351, 1.M_3^3. Occlusal view. × ⅓.

8. *Primelephas gomphotheroides* gen. et sp. nov. Type. PAL.LOTH. 351, 1.M_3^3. Lingual view. × ⅓.

9. *Primelephas gomphotheroides* gen. et sp. nov. Type. PAL.LOTH. 351, 1.M^3. Occlusal view. × ⅓.

10. *Primelephas gomphotheroides* gen. et sp. nov. Type. PAL.LOTH. 351, 1.M^3. Lingual view. × ⅓.

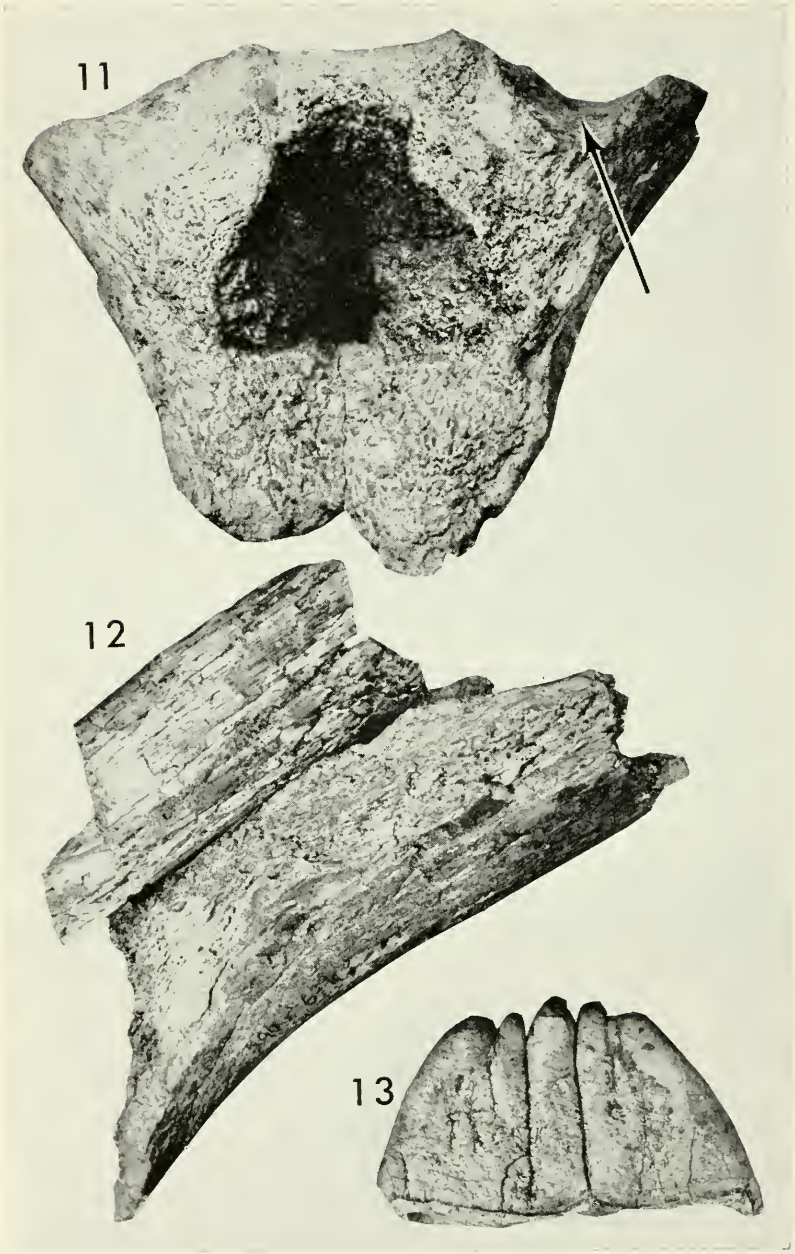

PLATE IV

PLATE IV

11. *Primelephas gomphotheroides* gen. et sp. nov. PAL.LOTH. 358, fragmentary symphysis showing ventral border of incisive alveolus (arrow). Anterior view. Approx. × ½.

12. *Primelephas gomphotheroides* gen. et sp. nov. PAL.LOTH. 358, symphysis with partial left incisor in place. Left-lateral view. Approx. × ½.

13. *Primelephas gomphotheroides* gen. et sp. nov. PAL.LOTH. 376, isolated molar plate, ?M^3. Anterior view. × ½.

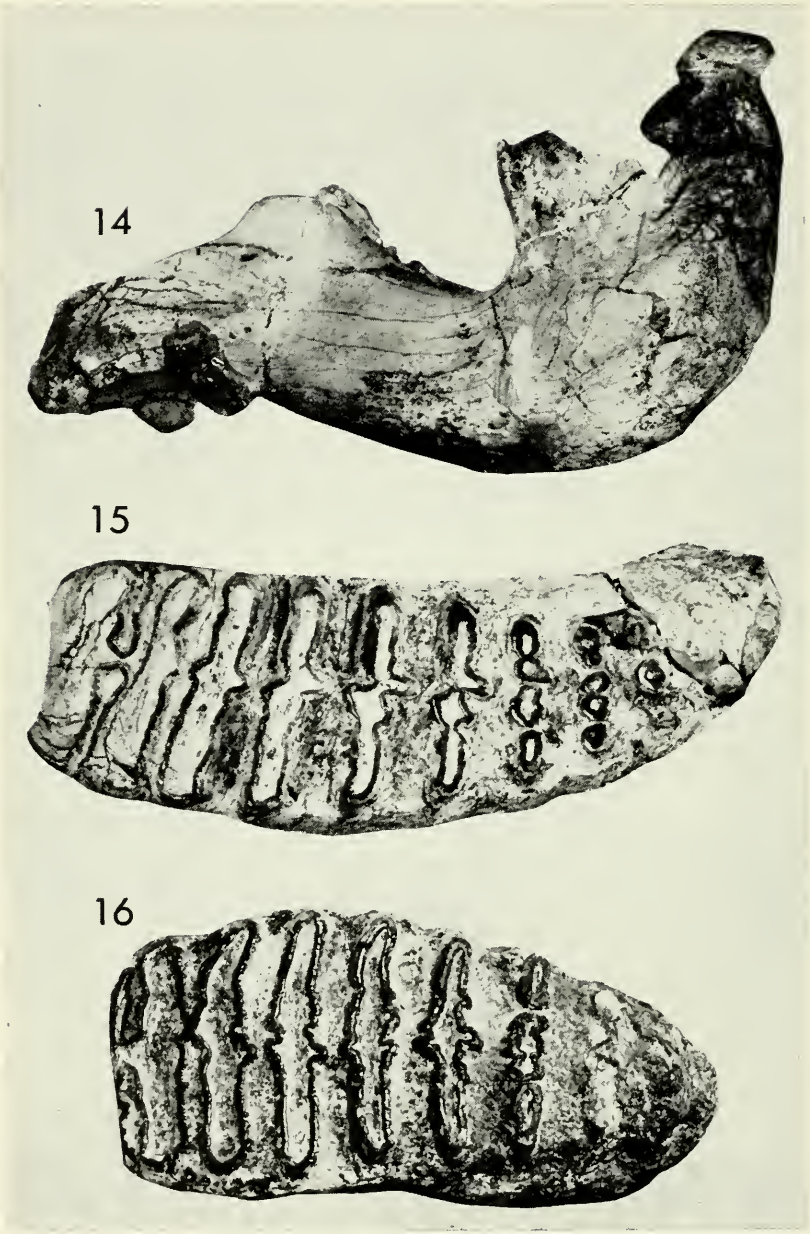

PLATE V

PLATE V

14. *Loxodonta adaurora* sp. nov. Type. PAL.KANAP. 385, mandible. Left-lateral view. Approx. × 1/7.

15. *Loxodonta adaurora* sp. nov. Type. PAL.KANAP. 385, r.M_3. Occlusal view. × ⅓.

16. *Loxodonta adaurora* sp. nov. Type. PAL.KANAP. 385, l.M^3. Occlusal view. × ⅓.

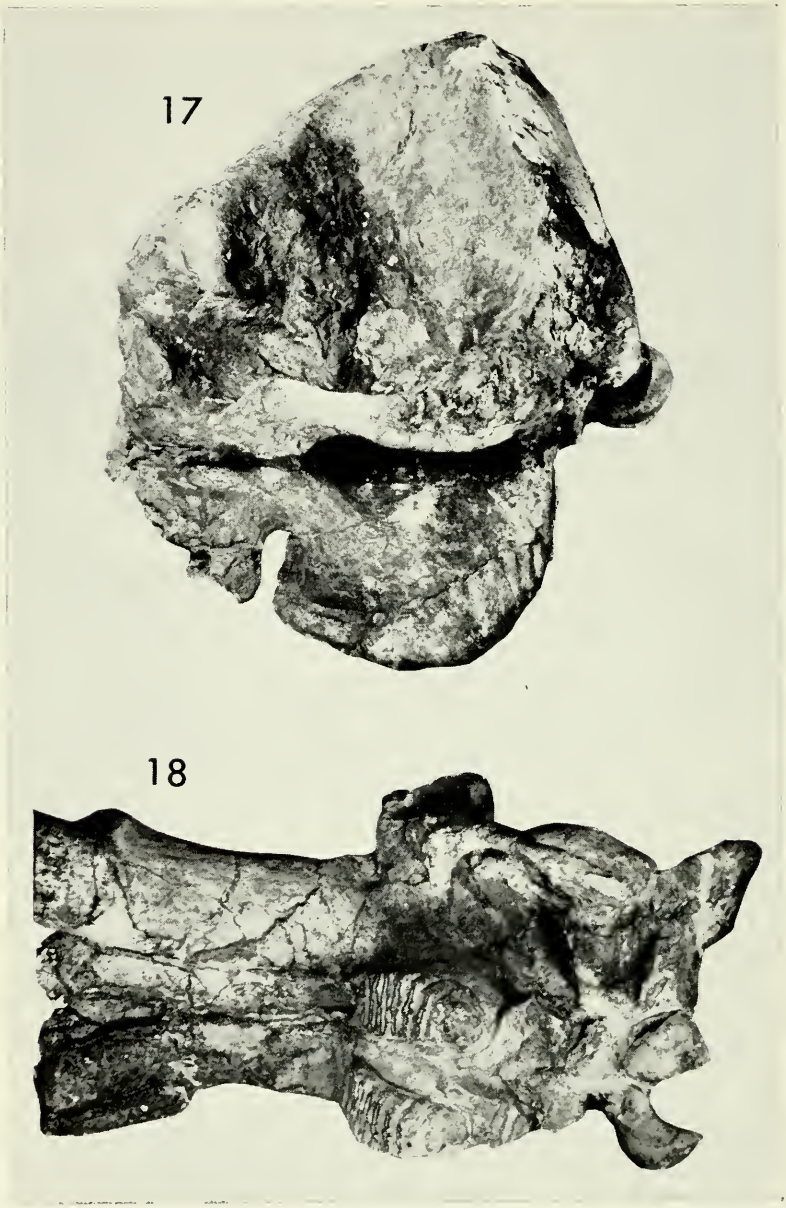

PLATE VI

PLATE VI

17. *Loxodonta adaurora* sp. nov. PAL.LOTH. 353, skull. Left-lateral view. Approx. × 1/9.

18. *Loxodonta adaurora* sp. nov. Type. PAL.KANAP. 385, skull. Ventral view. Approx. × 1/11.

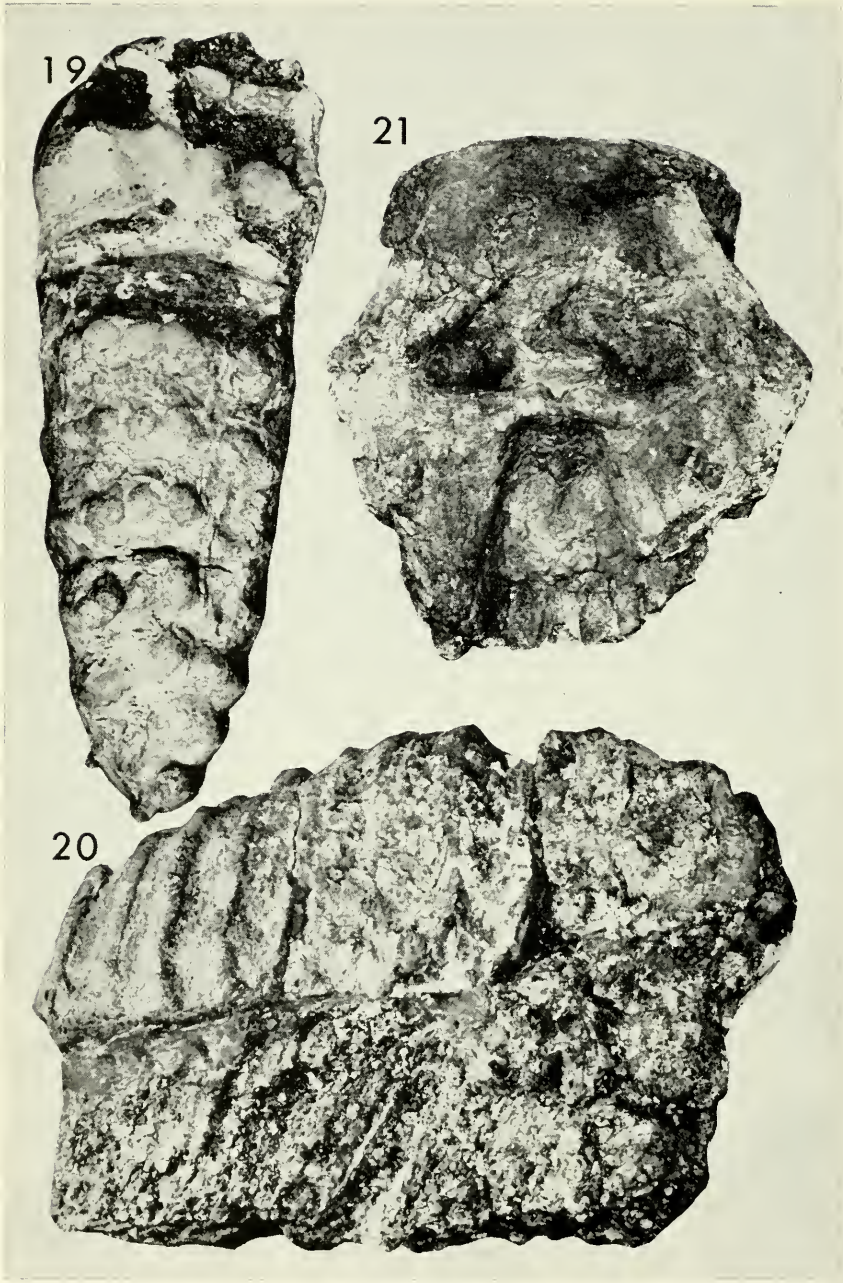

PLATE VII

PLATE VII

19. *Elephas ekorensis* sp. nov. Type. PAL.EKA. 424, r.M^3. Occlusal view. × ⅓.

20. *Elephas ekorensis* sp. nov. Type. PAL.EKA. 424, r.M^3. Lingual view. × ⅓.

21. *Elephas ekorensis* sp. nov. PAL.EKA. 422, skull. Anterior view. Approx. × 1/10.

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REDESCRIPTION OF POMACENTRUS OTOPHORUS POEY 1860, A VALID SPECIES FROM THE CARIBBEAN (PISCES: POMACENTRIDAE)

Robert W. Topp[1]

ABSTRACT. *Pomacentrus otophorus* Poey 1860 is restored to valid status and redescribed on the basis of material from Panama and Jamaica. It is distinguished from its western Atlantic congeners by a black opercular "earspot," soft vertical fin tips of bright yellow-orange, and the combination of short head, small eye, deep suborbital, absence of ocelli, and strong suborbital and preopercular serrations.

P. otophorus is unique among American damselfishes in that the adults are excluded from waters of sustained high salinity. This aspect of their ecology may have a bearing on the dissimilarity between Panama and Jamaica populations, as well as on the implied phyletic relationship between the Pomacentridae and Cichlidae.

INTRODUCTION

In late 1967 my attention was drawn to an unrecognized damselfish living in the Chagres River Estuary on the Caribbean coast of Panama. During subsequent months more than 60 specimens were collected from this and other Panama localities. In June, 1968, 10 additional specimens were obtained from Jamaica.

Upon review of nominal Caribbean species I found that this material seemed to agree in detail with the description of *Pomacentrus otophorus* Poey 1860. Examination of the holotype, USNM 4710, confirms the identity and thereby restores the species to valid status.

Poey's original description was drawn from a single 130 mm TL specimen and served as a model for his generic treatment. Jordan and Evermann's (1898: 1555) account was essentially an abridgment of Poey's original description.

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Rivas (1960) reviewed the Florida and western Bahamas species of *Pomacentrus,* but was unable to locate the holotype of *P. otophorus* at the Museum of Comparative Zoology (a depository of Poey's types). On the basis of Poey's unfigured description of its size, coloration, anterior profile, elongation of vertical fins, and number of pectoral rays, Rivas judged it to have been a large adult male of *P. leucostictus* Müller & Troschel 1848, and accordingly synonymized the two. Subsequent works have followed this synonymy by omitting *P. otophorus* from their lists.

METHODS

Panama specimens were obtained with Chem Fish Collector, a "bio-aquatic stupefier"; collecting was supplemented by diving observations. Methods for making counts and measurements follow those of Rivas (1960). In Table 1, positive or negative allometry resulting from ontogenetic change is indicated by (+) or (—). Color descriptions are based on 35 mm Kodachrome transparencies of fresh Panama material. Specimens have been placed in the following collections: USNM (United States National Museum), MCZ (Museum of Comparative Zoology), ANSP (Academy of Natural Sciences of Philadelphia), FMNH (Field Museum of Natural History, Chicago), UMML (Institute of Marine Sciences, University of Miami), FSBC (Florida [State] Board of Conservation, now the Florida Department of Natural Resources, St. Petersburg).

MATERIALS EXAMINED

Pomacentrus otophorus: USNM 4710 (holotype), 130 mm TL, Cuba, 1860. ANSP 109645, 102 mm, Port Antonio, Jamaica, E. C. Raney and D. P. de Sylva, 13 Oct. 1967. USNM 204607, (5) 39-88 mm, Port Antonio, 13 Oct. 1967. MCZ 46672, (4) 76-93 mm, Frenchman's Cove, Jamaica (11.9 ‰ salinity), H. Albrecht, 3 April 1968. MCZ 42737, (3) 32-62 mm, mouth of Chagres R., Canal Zone, Panama, I. and R. W. Rubinoff, 9 June 1962. MCZ 46671, (4) 44-95 mm, mouth of Chagres R., I. and R. W. Rubinoff, 13 Aug. 1966. USNM 204606, (14) 11-83 mm, mouth of Chagres R. (0 ‰ salinity), 24 Oct. 1967. FSBC 5596, 51 mm, Chagres R., Tarpon Club Boat Basin (fresh water), 24 June 1968. UMML 25066, (8) 14-56 mm, Panama Canal, Atlantic Third Locks (21.5 ‰ salinity), 4 Nov. 1967. FSBC 5597, (2) 16-32 mm, cleared and stained, Panama Canal, Atlantic Mine Docks (28.1 ‰ salinity), 4 Nov. 1967. FSBC

5598, (25) 13-79 mm, Panama Canal, Atlantic Mine Docks, 4 Nov. 1967. USNM 204608, (3) 40-64 mm, Panama Canal, Atlantic Mine Docks, 4 Nov. 1967. FSBC 5599, 49 mm, Chagres R., ½ km from mouth (0 ‰ salinity), 24 Oct. 1967. FMNH 69519, (9) 11-92 mm, mouth of Chagres R., (31.5 ‰ salinity), 13 March 1968.

Pomacentrus leucostictus: MCZ 25152, 70 mm, "Central America." MCZ 42728, (2) 53-62 mm, Galeta Pt., Canal Zone, Panama, I. and R. W. Rubinoff, 6 June 1961. MCZ 42731, 15 mm, Galeta Pt., I. and R. W. Rubinoff, 26 April 1962. MCZ 42732, (2) 20-50 mm, Galeta Pt., I. and R. W. Rubinoff, 26 April 1962. MCZ 42738, 18 mm, Galeta Pt., I. and R. W. Rubinoff, 20 June 1962. FSBC 5600, 69 mm, Galeta Pt., 7 Oct. 1967. 7 specimens, 15-70 mm, Devil's Beach, Ft. Sherman, Canal Zone, Panama, 12 Nov. 1967.

Pomacentrus fuscus: 10 specimens, 38-64 mm, Galeta Pt., Canal Zone, Panama, 25 July 1966.

Cichlasoma maculicauda: MCZ 46673, 104 mm, Chagres R., Tarpon Club Boat Basin (fresh water), Canal Zone, Panama, 24 June 1968. FSBC 5157, 62 mm, cleared and stained, Tarpon Club Boat Basin, 24 June 1968.

Pomacentrus otophorus Poey

Figure 1.

Pomacentrus otophorus Poey, 1860: 188 (original description, Cuba); 1868: 326 (coloration, Cuba)

Eupomacentrus otophorus, Jordan and Evermann, 1898: 1555 (description after Poey, Cuba). Jordan, Evermann and Clark, 1930: 414 (listed, Cuba).

Diagnosis

A euryhaline pomacentrid with short head, small eye, and deep suborbital. Dorsal fin XII (rarely XIII), 13-14 (rarely 12); anal II, 12 (rarely II, 11); pectoral rays 18 (occasionally 17 or 19). Suborbitals 4 and 5 and vertical margin of preopercle strongly serrate. Adults dark brown to blue-black; operculum with a black "earspot" at upper angle (*otophorus*=bearing an ear); distal one-third of soft dorsal, anal, and caudal fins bright yellow-orange; pectoral fin either unpigmented or tinged with orange except for a dark blotch at base. Juveniles blue-black with turquoise-blue stripes and spots; caudal fin and distal portions of soft vertical fins yellow, transparent at tips. Ocelli never present.

Description

A shallow-bodied species (depth 43-49% in SL), with dorsal outline more strongly rounded than ventral; anterior profile strongly convex. Caudal lobes rounded. Soft dorsal and anal fins rounded, both extending well beyond caudal fin base. Pelvics produced or not.

Dorsal and pelvic fins inserted well forward. Head short (29.7-33.3% in SL); orbital diameter small (7.5-11.5% in SL); suborbital deep (3.2-5.5% in SL). Table 1 lists proportional measurements for specimens greater than 39 mm.

Scales large, ctenoid; vertical fins with scale sheaths extending onto interradial membranes about halfway to fin margins. Pectoral fin with small scales covering base. Pelvic fin naked, but with a strong ensiform scale at each fin axil and another between the fins. Cheeks scaled. Jaws, preorbital region, and suborbitals 1-3 naked; scale of suborbital 4 embedded when present. Lateral line terminating below base of first soft dorsal ray. Teeth uniserial, close-set, entire, similar in both jaws.

Fourth and fifth suborbital ossicles bearing 0 to 7 (mean, 2.4) moderate to strong posteriorly directed serrae, usually present in specimens 45-50 mm or larger. Vertical limb of preopercle with 5 to 15 (mean, 10.7) strong serrae; angle smoothly rounded. Dorsal spines 12, 1 of 60 with 13; dorsal rays 13 or 14, 2 of 60 with 12; anal rays 12, 2 of 60 with 11; pectoral rays 17-19. Body scales 26-29; tube-bearing scales in lateral line 16-19. Gill rakers on lower limb (including raker at angle), 8-10; on upper limb, 2-3. Trunk vertebrae 11; caudal, 15. Cheek scales 3-4 between suborbital edge and angle of preopercle. Distribution of meristic characters is shown in Table 2.

Coloration

Typical of many pomacentrids, *P. otophorus* changes color with ontogeny, tending toward a less conspicuous adult.

Small juveniles (<15 mm) of blue-black ground color, with turquoise-blue markings arranged as follows (Fig. 2): 1) a conspicuous arc along dorsal one-third of corneal perimeter, colinear with a postorbital stripe, continuing as a row of spots along scale row just above lateral line, extending to posterior dorsal fin base; 2) successively less distinct rows immediately below lateral line, each row extending caudad from operculum, but failing to reach peduncle; 3) prominent markings on scales bordering dorsal fin

base, with spots extending onto scales of interradial membranes; 4) a pair of variably broken lines on head and nape extending from premaxillary groove posteriad between orbits and converging at dorsal fin origin; 5) several markings arranged circumorbitally, including a conspicuous line on vertical limb of preopercle. Pectoral fin either transparent or tinged with orange, except at base. Pelvic fin pigmented, sometimes transparent or orange near tip. Posterior tip of opercle transparent. Caudal yellow, becoming transparent near tips of rays. Ocelli absent.

Larger juveniles with reduced turquoise-blue markings, which by 30 mm appear as small circular blue spots on scales above lateral line, on operculum, around eye, and occasionally elsewhere. Preopercular markings and those below lateral line now barely visible; paired lines on head reduced in breadth. Operculum developing a blue-black "earspot" resembling that of the primary freshwater centrarchid fishes of North America, and shared by a few western Pacific pomacentrid species.

Subadults and adults with head and body dark brown to sooty blue-black. Centers of scales black, producing vertical striations. Blue markings indistinct or absent. Distal one-third to two-thirds of soft vertical fins yellow-orange, this proportion generally decreasing with size; dark ground color encroaching well distad along interradial membranes. Pectoral fin transparent or tinged with orange, except for a black inverted triangle at base. Earspot now prominent, blue-black to black. Opercular spine and fleshy flap unpigmented. Sexual dichromism not apparent in preserved specimens.

Most Panama specimens with a pair of dusky lines on caudal fin, generally present by 35 mm, often obscured by extensive body pigmentation in large fish; their extent and prominence variable, but occurring in a constant position relative to caudal skeleton: counting ventrad on third hypural, ventral line occupies membrane between third and fourth lepidotrichs; counting dorsad on fourth hypural, dorsal line lies between fourth and fifth lepidotrichs. These lines not present on Jamaica specimens.

Comparisons

Pomacentrus otophorus differs from all other western Atlantic congeners by its distinctive "earspot." Fresh adults are quickly distinguished by their bright yellow-orange fin tips, juveniles by their bright turquoise-blue markings. Additional differences include the small number of dorsal and anal rays, and the combination of short head, small eye, and deep suborbital.

Although *P. otophorus* closely resembles *P. leucostictus* in general physiognomy, preserved material is readily distinguished by the suborbital and preopercular serrations and the persistent earspot. Subadults are further separated by the lack of ocelli. Comparative morphometric and meristic data for *P. leucostictus* from Panama is included in Tables 1 and 2.

Geographical Variation

Although comparative material is limited, differences between Panama and Jamaica collections are readily apparent. Caudal lines, for example, present on most Panama specimens greater than 35 mm, are lacking in similar material from Jamaica. Ranges of measurements and counts for specimens from the two populations are included in Tables 1 and 2. Using "t" tests on material of comparable size, significant differences ($P=0.01$, d. f. $=28$) can be recognized in snout length ($t=4.78$) and interorbital width ($t=4.79$). Figure 3 shows separation of the two populations on the basis of these two characters.

To evaluate the taxonomic status of the two populations, inter- and intraspecific differences among closely related species were assessed, following suggestions of Mayr (1969: 197):

1) Degree of difference among closely related sympatric species was evaluated by comparing Panama collections of *Pomacentrus otophorus, P. leucostictus,* and *P. fuscus.*

2) Degree of difference between geographically separated populations of *P. leucostictus* and of *P. fuscus* were evaluated by comparing Panama data with those of Rivas (1960) for similar material from Florida-western Bahamas.

The coefficient of difference, CD, defined as the difference between means divided by the sum of standard deviations, was determined for the same 10 sets of characters in each comparison. Sums of the 10 coefficients, SCD, for the various combinations are:

Sympatric species	
P. otophorus vs. *P. fuscus*	13.91
P. otophorus vs. *P. leucostictus*	8.56
P. leucostictus vs. *P. fuscus*	7.41
Widespread populations	
P. fuscus (Panama vs. Florida)	4.47
P. otophorus (Panama vs. Jamaica)	3.89
P. leucostictus (Panama vs. Florida)	2.46

The observed differences between Panama and Jamaica populations of *P. otophorus* are consistent with those of widespread populations of related species, but do not approach those of interspecific rank. The two populations are, on this basis, judged to be conspecific.

Ecology and Behavior

Recognized species of *Pomacentrus* in the western Atlantic are, as adults, typically obligate coral reef dwellers, and are thus principally stenohaline. Juveniles of some, however, regularly inhabit lagoons and rock pools, where they are exposed to fluctuating salinities. Representatives of the genera *Abudefduf* and *Nexilarius* are still more broadly tolerant of environmental extremes, especially as juveniles, and can be experimentally maintained in fresh water for indefinite periods.

P. otophorus is unique among western Atlantic pomacentrids since the adults are excluded from waters of sustained high salinity. Jamaica specimens were collected in salinity of 11.9 ‰, whereas Panama specimens were collected in salinities of 0 to 31.5 ‰. The species is common in the Atlantic end of the Panama Canal and adjacent brackish waters, where salinities of 21.5 to 28.1 ‰ were recorded, and in the Chagres River Estuary, where salinities ranged over the full regime of 0 to 31.5 ‰. Specimens have also been collected from the river proper, and from the Tarpon Club Boat Basin adjacent to Gatun Dam spillway, over 10 km upstream. Figure 4 shows Panama collection localities.

In waters of sustained high salinity ($>$ 30 ‰) its absence is notable; not a single specimen has been collected in coral reef habitats during some eight years of sampling by the Smithsonian Tropical Research Institute.

In Panama, *P. otophorus* was collected from waters subject to occasional high turbidity and turbulence. In the Panama Canal and Chagres estuary, substrate is of moderately sedimented rubble; in the Third Locks, rubble and mud. The Tarpon Club Boat Basin is lacustrine, of good transparency, with dense growths of phanerogams along the shore and heavy algal growth on the docks and pilings. A single 51 mm specimen of *P. otophorus* was collected there on 24 June 1968, along with the following associates, now in MCZ and FSBC collections:

1 *Gambusia episcopi,* 35 mm
2 *Cichlasoma maculicauda,* 62-104 mm

12 *Eucinostomus* sp., 35-58 mm
3 *Diapterus rhombeus,* 30-43 mm
4 *Centropomus pectinatus,* 88-110 mm
20 *Gobionellus* sp., 22-55 mm
8 *Microeleotris* sp., 17-40 mm
1 *Eleotris isthmensis,* 22 mm

P. otophorus is exclusively herbivorous throughout life, as far as is known. The only animal material present in gut samples was small invertebrates probably ingested incidental to grazing.

In Panama, reproductive activity was not observed. In Jamaica, the color pattern of courting males apparently involves a concentration of dark pigment in the anterior parts, while the posterior body and vertical fins remain yellow. Nest-guarding males retain the yellow in parts of each scale (Alan Emery, personal communication, 27 June 1968).

Distribution

Although the degree of difference between Panama and Jamaica populations of *P. otophorus* is consistent with that demonstrated between Panama and Florida populations of related species, only about one-half the latitudinal distance is involved, suggesting that intraspecific heterogeneity in *P. otophorus* may exceed that of its Caribbean congeners. There is, indeed, ample ecological basis for such an expectation:

The exclusion of *P. otophorus* from waters of persistently high salinity may effectively give rise to geographically isolated demes along the Caribbean coast of Central America. If its reproductive activities include the nest building and parental care typical of other damselfishes, genetic exchange between demes is probably limited. Their Caribbean congeners, however, have no extrinsic salinity barriers to continuous populations along the coast. This greater freedom of gene flow can be expected to result in more panmictic populations.

Relationships

A close relationship has long been suspected between the pantropical marine Pomacentridae and the secondary freshwater Cichlidae. The two share a number of anatomical similarities (e. g., united lower pharyngeals) and have been united into the order Chromides by Jordan and Evermann (1898: 1511) and Jordan (1923: 218). They are mutually unique among the Perciformes

in having but a single pair of external nostrils. Despite their divergence of habitat, the two families also show close similarities in reproduction and behavior (Wickler, 1967).

In Panama, one specimen of *P. otophorus* (FSBC 5596) was taken in company with two specimens of the cichlid fish, *Cichlasoma maculicauda;* gut analyses showed that both species had been feeding on filamentous green algae. This ecological overlap strengthens the implication of close phyletic proximity for the two families.

ACKNOWLEDGMENTS

I am particularly indebted to Ira and Roberta W. Rubinoff for their generosity and assistance throughout this study, and to Alan R. Emery for providing specimens from Jamaica and for reading the manuscript. I thank Stanley H. Weitzman, Robert H. Gibbs, Jr., and Robert Kanazawa for providing information on the holotype, and Mrs. Myvanwy Dick for the loan of specimens. I am also grateful to Giles W. Mead, C. Richard Robins, and Dale S. Beaumariage for critically reading the manuscript. The financial support of a Smithsonian Predoctoral Internship is gratefully acknowledged.

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(Received 29 October 1969.)

TABLE 1

Proportional characters of *Pomacentrus otophorus* and *P. leucostictus*

(+)=positive allometry; (−)=negative allometry

Character	*P. otophorus* Holotype (Cuba) USNM 4710	*P. otophorus* Panama (20)		*P. otophorus* Jamaica (10)		*P. leucostictus* Panama (6)	
		Range	Mean	Range	Mean	Range	Mean
Standard length (mm)	103	41-95	72	39-102	74	32-70	56
Predorsal length (−)	359	353-397	371	374-415	388	361-394	379
Preanal length (−)	714	652-706	669	670-717	691	675-702	689
Prepelvic length (−)	388	361-383	372	362-397	380	376-431	398
Head length (−)	291	297-314	305	299-333	312	301-319	309
Snout length (+)	107	80-109	96	99-116	107	78-95	87
Maxillary length (−)	83	78-95	84	82-94	86	83-92	88
Orbit diameter (−)	73	76-98	86	75-115	86	86-116	97
Suborbital width (+)	49	32-51	46	38-55	48	25-37	33
Interorbital width (−)	91	94-108	101	87-96	92	84-97	88
Body depth	437	439-486	458	433-483	456	425-472	450
Caudal peduncle depth	160	156-168	162	145-168	154	140-154	149
Pectoral fin length	262	268-298	283	259-307	283	263-277	271
Pelvic fin length	291	273-332	305	270-338	313	292-360	326
Anal fin length (+)	393	402-464	429	358-433	399	381-437	416
Upper caudal lobe length (+)	286	286-342	325	286-349	317	308-366	338

TABLE 2

Distribution of meristic characters in *Pomacentrus otophorus* and *P. leucostictus*

Dorsal rays	No.	12	13	14	15	16	Range	Mean
P. otophorus (Panama)	50	1	23	26			12-14	13.5
P. otophorus (Jamaica)	10	1	8	1			12-14	13.0
P. leucostictus (Panama)	15			1	12	2	14-16	15.1

Anal rays	No.	11	12	13	14	Range	Mean
P. otophorus (Panama)	49	2	47			11-12	13.0
P. otophorus (Jamaica)	10		10			12	12.0
P. leucostictus (Panama)	15		3	8	4	12-14	13.1

Pectoral rays	No.	17	18	19	Range	Mean
P. otophorus (Panama)	50	6	40	4	17-19	18.0
P. otophorus (Jamaica)	10		10		18	18.0
P. leucostictus (Panama)	15		10	5	18-19	18.3

Lateral line scales	No.	16	17	18	19	20	Range	Mean
P. otophorus (Panama)	49	1	6	32	10		16-19	18.0
P. otophorus (Jamaica)	10		1	4	5		17-19	18.4
P. leucostictus (Panama)	15			2	7	6	18-20	19.3

Body scales	No.	26	27	28	29	Range	Mean
P. otophorus (Panama)	49	1	14	33	1	26-29	27.7
P. otophorus (Jamaica)	10		1	8	1	27-29	28.0
P. leucostictus (Panama)	15		2	10	3	27-29	28.1

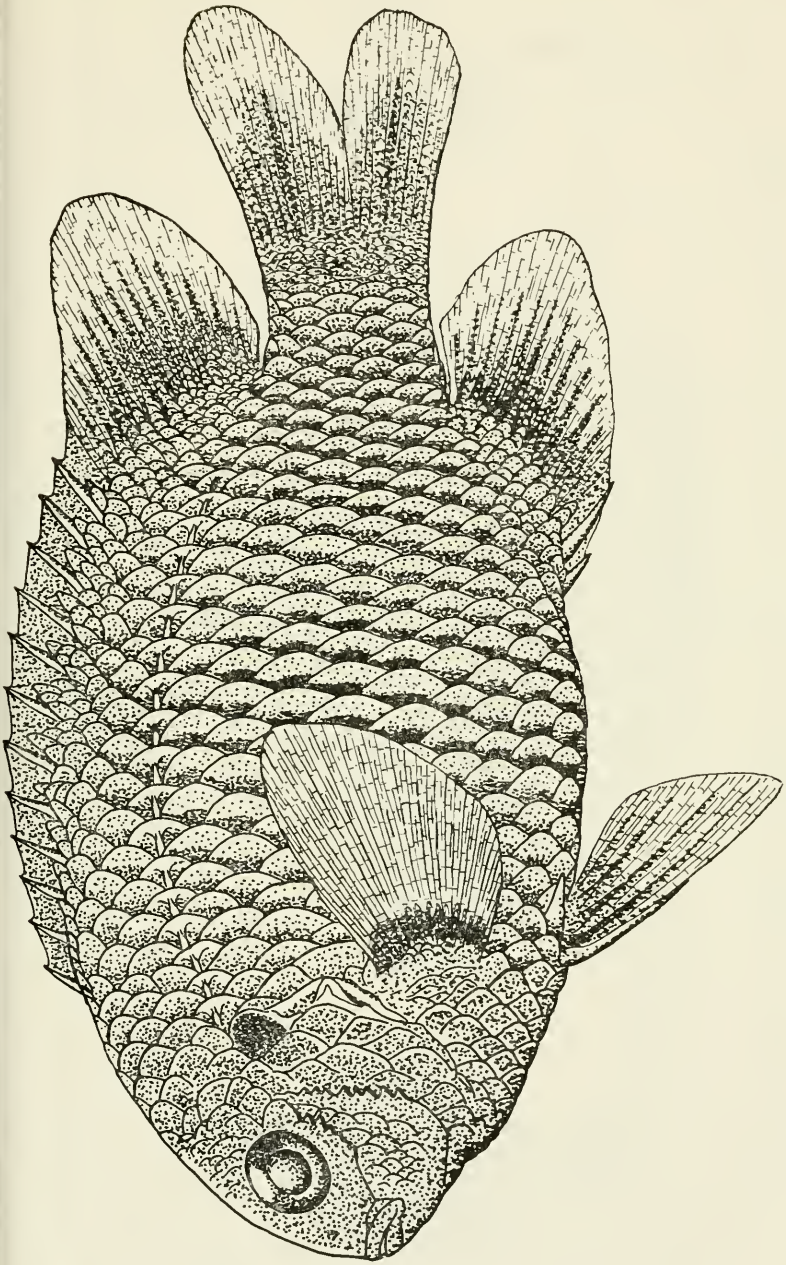

Figure 1. *Pomacentrus otophorus*, 78 mm SL, mouth of Chagres R., Panama, 24 Oct. 1967.

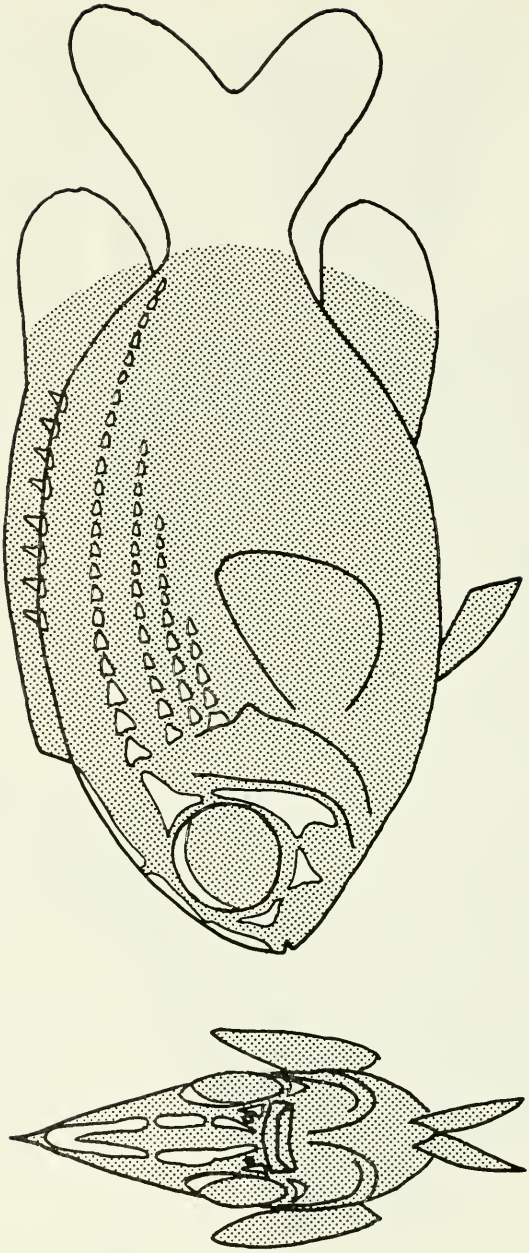

Figure 2. *Pomacentrus otophorus*, juvenile, showing extent and pattern of pigmentation. Not drawn to scale.

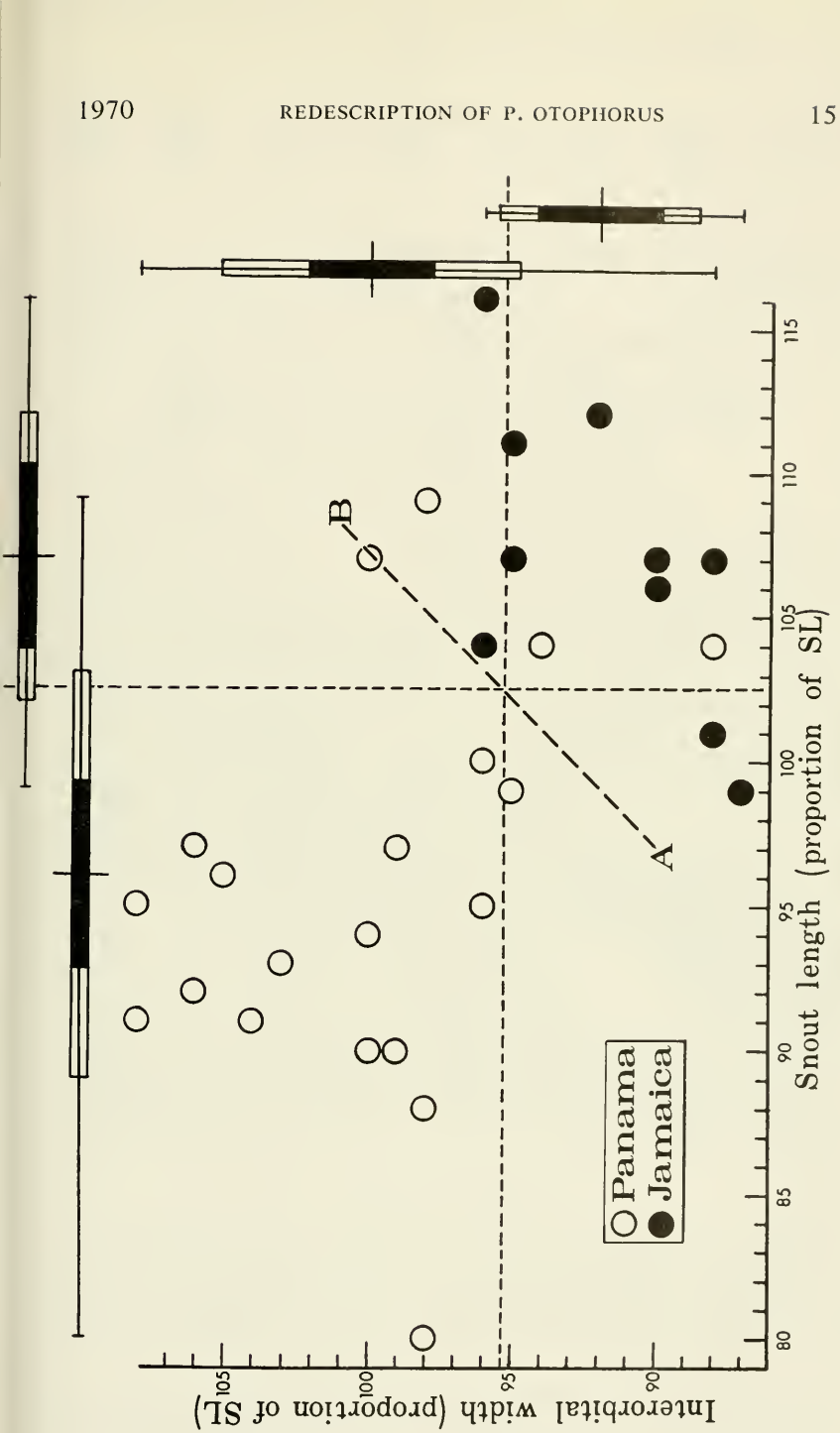

Figure 3. Separation of Panama and Jamaica populations of *Pomacentrus otophorus* on basis of relative snout length and interorbital width. Range, mean, standard deviation, and 2 standard errors on either side of mean are shown. AB=line of best separation.

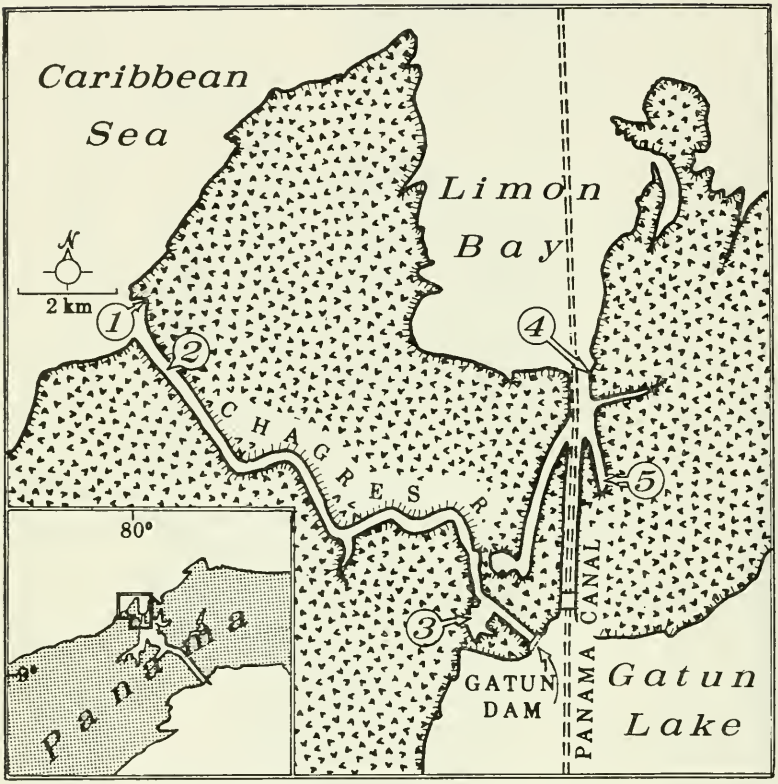

Figure 4. Panama collection localities: 1. Mouth of Chagres R., 2. Chagres R., 1/2 km from mouth, 3. Chagres R., Tarpon Club Boat Basin, 4. Panama Canal, Atlantic Mine Docks, 5. Panama Canal, Atlantic Third Locks.

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PALEOECOLOGY OF A LATE CRETACEOUS VERTEBRATE COMMUNITY FROM MONTANA[1]

Richard Estes and Paul Berberian

ABSTRACT. At least 78 species representing five classes of vertebrates occur at the Bug Creek Anthills locality, in the Hell Creek Formation, McCone County, Montana. The fauna closely resembles that from the Lance Formation of Wyoming, also of late Cretaceous age.

Quantitative paleoecological techniques originally devised for late Cenozoic mammals required only slight modification to prove useful when applied to the late Cretaceous sample. The resulting analysis shows that at Bug Creek Anthills, fishes, aquatic salamanders, and mammals are more abundant than the amphibious or terrestrial turtles, dinosaurs, and (especially) lizards, when compared with these groups in the Lance Formation fauna. While the latter was probably deposited within the general environment of a swamp forest with relatively small watercourses, the Bug Creek Anthills fauna seems to have been laid down in the relatively deeper waters of major rivers issuing from those lowland swamps. Gar and bowfin fish, and elongated salamanders, are dominant species in the aquatic community nearest to the site of deposition; some of the mammals seem to have been part of a nearby riverbank community.

Excluding birds, 73 genera occur in the Cretaceous sample while 128 genera occur in its closest modern analogue, the Recent fauna of southern Louisiana. If this comparison is valid, the fossil sample may represent about two-thirds of the generic diversity present on the subtropical Cretaceous floodplain.

INTRODUCTION

Recent work by Dr. Robert Sloan and his associates has resulted in recovery of a large collection of vertebrate fossils from a series of late Cretaceous localities in the upper one-third of the Hell Creek Formation, McCone County, Montana (Sloan and Van

[1] Fossil vertebrates from the late Cretaceous Hell Creek Formation, Montana: Contribution No. 9.

Valen, 1965). The lower vertebrates from this part of the section have been described in a series of papers listed by Estes, Berberian, and Meszoely (1969). The fossil sample is from a quarry, and the specimens were carefully concentrated by the use of washing and screening techniques (McKenna, 1962). All fossil material was removed and an attempt was made to identify each specimen; it is thus possible to make comparison with the similarly-collected sample from the Lance Formation of Wyoming (Estes, 1964), and to apply techniques of paleoecological analysis developed by Shotwell (1955). A substantial faunal similarity between the two samples indicates a similar environment and inferred climate; essential contemporaneity of the two localities further enhances the paleoecological significance of such a comparison.

Bug Creek Anthills (BCA) is the richest of the Hell Creek localities on and near Bug Creek that were discovered by Sloan. A collection from this locality made by a field party of the Museum of Comparative Zoology with the aid of Sloan and his field crew was used for the numerical analysis discussed below. The total faunal list was determined by examination of collections made by a number of institutions (Estes, et al., 1969). BCA is a quarry site that occurs in a cross-bedded stream channel within the upper one-third of the Hell Creek Formation, about 80 feet below the coal bed used locally as the arbitrary mapping boundary between the Cretaceous and Tertiary (Sloan and Van Valen, 1965).

FAUNAL LIST

This list includes only species from BCA and other localities in the section on Bug Creek; those not present in BCA are followed by locality data in brackets. The list of mammals has been provided by Sloan, with additions by W. A. Clemens, Jr. (1969, pers. comm.). With the further addition of the unidentifiable ornithomimid material cited by Osborn (1916), the ankylosaurid *Ankylosaurus magniventris* (Brown, 1908), and the panoplosaurid teeth noted by Brown (1907: 842) this becomes the most complete list of valid Hell Creek Formation vertebrates available. *Lamna* sp. was also cited as present by Brown (1907: 842) but the single specimen mentioned is no longer available to substantiate the identification.

VERTEBRATES FROM THE BUG CREEK LOCAL FAUNAS, HELL CREEK FORMATION

CLASS CHONDRICHTHYES
ORDER SELACHII
Family Hybodontidae
Lonchidion selachos Estes

ORDER BATOIDEA
Family Pristidae
Ischyrhiza avonicola Estes [Harbicht Hill]
Family Dasyatidae
Myledaphus bipartitus Cope

CLASS OSTEICHTHYES
INFRACLASS CHONDROSTEI
ORDER ACIPENSERIFORMES
Family Acipenseridae
Acipenser eruciferus Cope
Protoscaphirhynchus squamosus Wilimovsky [Rock Creek, SE¼ Sect. 36, T23N, R43E]
Family Polyodontidae
Paleopsephurus wilsoni MacAlpin

INFRACLASS HOLOSTEI
ORDER ASPIDORHYNCHIFORMES
Family Aspidorhynchidae
Belonostomus longirostris (Lambe)

ORDER AMIIFORMES
Family Amiidae
Amia fragosa (Jordan)
Amia (=*Protamia*) sp.

ORDER AMIIFORMES?
Family Palaeolabridae
Palaeolabrus montanensis Estes

ORDER LEPISOSTEIFORMES
Family Lepisosteidae
Lepisosteus occidentalis Leidy

INFRACLASS TELEOSTEI
ORDER ELOPIFORMES
Family Elopidae
unidentified genus and species

Family Phyllodontidae
cf. Paralbula casei Estes

Family Albulidae
Coriops amnicolus Estes

ORDER PERCIFORMES
Family Sciaenidae
Platacodon nanus Marsh

TELEOSTEI *incertae sedis*

CLASS AMPHIBIA
ORDER CAUDATA
SUBORDER AMBYSTOMATOIDEA
Family Scapherpetontidae
Scapherpeton tectum Cope
Lisserpeton bairdi Estes
Family Prosirenidae
Prodesmodon copei Estes
Family Batrachosauroididae
Opisthotriton kayi Auffenberg

SUBORDER SALAMANDROIDEA?
Family Amphiumidae
Proamphiuma cretacica Estes

SUBORDER MEANTES
Family Sirenidae
Habrosaurus dilatus Gilmore

ORDER SALIENTIA
Family Discoglossidae
Scotiophryne pustulosa Estes
cf. Barbourula sp.
undescribed genus and species
Family Pelobatidae?
Eopelobates? sp.

CLASS REPTILIA
ORDER EOSUCHIA
Family Champsosauridae
Champsosaurus sp.

ORDER TESTUDINATA
- Family Baenidae
  - *Eubaena cephalica* Hay
  - undescribed genus and species 1
  - undescribed genus and species 2
- Family Dermatemydidae
  - *Compsemys victa* Leidy
  - *Adocus* sp.
- Family Testudinidae
  - Subfamily Emydinae?
    - unidentified genus and species
- Family Trionychidae
  - *Trionyx* sp.

ORDER SAURIA
- SUBORDER SCINCOMORPHA
  - Family Teiidae
    - *Chamops segnis* Marsh
    - *Leptochamops denticulatus* (Gilmore)
    - *Haptosphenus placodon* Estes
    - *Peneteius aquilonius* Estes
  - Family Scincidae?
    - *Contogenys sloani* Estes
- SUBORDER ANGUIMORPHA
  - Infraorder Diploglossa
    - Family Xenosauridae
      - *Exostinus lancensis* Gilmore
    - Family Anguidae
      - *Pancelosaurus piger* (Gilmore)
    - Family Parasaniwidae
      - *Parasaniwa wyomingensis* Gilmore
      - *Paraderma bogerti* Estes
    - Diploglossa *incertae sedis*
      - *Colpodontosaurus cracens* Estes
  - Infraorder Platynota
    - Family Varanidae
      - *Palaeosaniwa, cf. P. canadensis* Gilmore

Sauria? *incertae sedis*
- Family *incertae sedis*
  - *Cuttysarkus mcnallyi* Estes

ORDER SERPENTES
Superfamily Booidea
Family Aniliidae
Coniophis precedens Marsh
Family Boidae
unidentified genus and species

ORDER CROCODILIA
SUBORDER EUSUCHIA
Family Crocodilidae
Subfamily Crocodilinae
Leidyosuchus sternbergi Gilmore
Thoracosaurus neocesariensis (DeKay) [SW¼ Sect. 28, T24N, R44E]
Subfamily Alligatorinae
Brachychampsa montana Gilmore

ORDER SAURISCHIA
SUBORDER THEROPODA
INFRAORDER COELUROSAURIA
Family Coeluridae?
unidentified genus and species
Paronychodon lacustris Cope

THEROPODA? *incertae sedis*
undescribed genus and species

INFRAORDER DEINONYCHOSAURIA
Family Dromaeosauridae?
unidentified genus and species

INFRAORDER CARNOSAURIA
Family Tyrannosauridae
Gorgosaurus lancensis Gilmore? [Bug Creek West; Harbicht Hill]
Tyrannosaurus rex Osborn [NE¼ Sect. 7, T22N, R43E]

ORDER ORNITHISCHIA
SUBORDER ORNITHOPODA
Family Hypsilophodontidae
Thescelosaurus neglectus Gilmore
Family Pachycephalosauridae?
unidentified genus and species
Family Hadrosauridae
Anatosaurus copei Lull and Wright

SUBORDER CERATOPSIA
Family Ceratopsidae
Triceratops prorsus Marsh

CLASS AVES
ORDER CHARADRIIFORMES
Family Cimolopterygidae
Cimolopteryx sp.

CLASS MAMMALIA
SUBCLASS ALLOTHERIA
ORDER MULTITUBERCULATA
Superfamily Ptilodontoidea
Family Ectypodidae
Cimexomys minor Sloan and Van Valen
Mesodma formosa (Marsh)
Mesodma thompsoni Clemens
Family Ptilodontidae
Cimolodon nitidus Marsh
Essonodon browni Simpson
Superfamily Taeniolabidoidea
Family Cimolomyidae
Cimolomys gracilis Marsh
Meniscoessus borealis Simpson
Eucosmodontidae
Stygimys kuszmauli Sloan and Van Valen
Family Taeniolabididae
Catopsalis joyneri Sloan and Van Valen

SUBCLASS METATHERIA
ORDER MARSUPIALIA
Family Didelphidae
Didelphodon vorax Marsh
Alphadon marshi Simpson
A. wilsoni Lillegraven
Pediomys elegans Marsh
P. krejcii Clemens
P. hatcheri (Osborn)
P. cooki Clemens
P. florencae Clemens
Glasbius intricatus Clemens

SUBCLASS THERIA
INFRACLASS EUTHERIA
ORDER DELTATHERIDIA
Family Palaeoryctidae
Cimolestes incisus Marsh
C. magnus Clemens and Russell
Procerberus formicarum Sloan and Van Valen

ORDER INSECTIVORA
Family Leptictidae
Gypsonictops hypoconus Simpson
G. illuminatus Lillegraven?

ORDER PRIMATES
Family Paromomyidae
Purgatorius ceratops Van Valen and Sloan [Harbicht Hill]

ORDER CONDYLARTHRA
Family Arctocyonidae
Protungulatum donnae Sloan and Van Valen
P. spp. [Bug Creek West; Harbicht Hill]

INTERPRETATION OF THE FAUNA

Introduction

The Bug Creek Anthills local fauna from the Hell Creek Formation differs only in detail from that of the Lance Formation (Estes, 1964).[1] There are few Lance species that do not also occur in the BCA sample, but the latter includes some additional forms of special interest as well as some significant differences in relative abundance (Table 1) from Lance forms (see also Estes et al., 1969: table 1).

Because time of deposition of the upper parts of both the Lance Formation and the Hell Creek Formation was essentially synchronous, because their lithologies are similar and indicate similar coastal floodplain environments of deposition, because both local faunas bear a similar relationship to late Cretaceous mid-continental seaways, because their vertebrate faunas are very similar, and because the two samples were carefully collected using the same techniques, an unusual opportunity is provided for comparing these samples.

The Bug Creek sample was carefully collected by the use of washing and screening techniques, all fossil material was retained, and an attempt was made to identify each fossil fragment; it was therefore possible to apply the community analysis method devised by Shotwell (1955, 1958). Since only a few aspects of Shotwell's method were applied to the Lance Formation sample by Estes (1964), we have used American Museum of Natural History Lance Formation samples from V5620 and V5711 to make some additional comparisons for this study.

The time spent in sorting and identifying the thousands of specimens used in this study (including collections from all institutions) has been the major factor delaying completion of this series of papers. However, we agree with Shotwell (1963: 9, in reply to Wilson, 1960: 9) that careful sorting, however time-consuming, is a procedure necessary to any quantitative study and that the time involved in this activity is not a valid objection to his method. Shotwell developed his method for analysis of late Cenozoic mammalian faunules; it is our intent to test its utility when applied to late Cretaceous lower vertebrate samples. Voorhies (1969) has offered some cogent criticisms of Shotwell's method. Some of these

[1] Comparisons with the Lance Formation refer only to the two major localities V5620 and V5711 (Clemens, 1963).

TABLE 1

Abundance and completeness of vertebrate remains from Bug Creek Anthills, Hell Creek Formation, Montana, with some comparative figures for V5620, Lance Formation, Wyoming.

	Bug Creek Anthills, Hell Creek Formation[4]						*Lance Formation*[3]	
	MNI	*RA*	*NS*	*ENE*	*CNS*	*RC*	*MNI*	*RA*
Lonchidion (C)	1	.2	3	130	2.3	2.3	3	.4
Myledaphus	1	.2	86	400	21.5	7.2	1	.1
Squatirhina	—	—	—	—	—	—	1	.1
Ischyrhiza	—	—	—	—	—	—	1	.1
Acipenser	7	1.0	66	80	82.5	11.8	1	.1
Paleopsephurus (A)	3	.4	8	56	14.3	4.8	1[2]	.1
"Protamia" (D)	1	.2	1	170	.6	.6	1	.1
Amia	94	13.1	2024	170	1190.6	12.7	103	15.2
Belonostomus (D)	1	.2	1	200	.5	.5	3	.4
Lepisosteus	25	3.5	1790	200	895.0	35.8	7	1.0
Coriops (D)	3	.4	4	200	2.0	.7	22	3.2
cf. Paralbula (D)	1	.2	1	170	.6	.6	—	—
Palaeolabrus	7	1.0	72	200	36.0	5.1	—	—
Elopidae	1	.2	1	170	.6	.6	1	.1
Platacodon (C)	2	.3	8	200	4.0	2.0	42	7.0
Habrosaurus	9	1.3	100	90	111.1	12.4	71	10.5
Opisthotriton	107	14.9	980	90	866.7	8.1	41	6.0
Scapherpeton	61	8.6	744	70	1062.9	17.4	22	3.2

Lisserpeton	72	10.1	275	70	392.9	5.5	1[2]	.1
Prodesmodon	2	.3	10	75	13.3	6.7	11	1.6
Proamphiuma	2	.3	15	100	15.0	7.5	—	—
Scotiophryne	6	.9	32	60	53.3	8.9	1[2]	.1
cf. Barbourula	1	.2	1	60	1.7	1.7	1	.1
other frogs (B)	3	.6	8	60	6.6	<7[1]	12	1.7
Adocus (C)	1	.2	5	190	2.6	2.6	—	—
Basilemys	—	—	—	—	—	—	1	.1
Compsemys (A)	1	.2	17	190	8.9	4.5	1	.1
Trionyx (A)	1	.2	10	190	5.3	5.3	1	.1
Eubaena	3	.4	85	190	44.7	14.9	1	.1
other baenids (E)	4	.6	85	190	44.7	<12[1]	1	.1
Emydinae (D)	3	.3	5	190	2.6	1.3	1	.1
Brachychampsa (D)	1	.2	150	200	1.4	1.4	1	.1
Leidyosuchus (D)	1	.2	150	200	1.4	1.4	1	.1
Champsosaurus (A)	2	.3	11	130	8.5	4.2	1	.1
dinosaurs (A-D)	7	.2	131	var.	19.3	<4[1]	8	1.2
Peneteius (D)	1	.2	1	120	.8	.8	—	—
Champs (C)	3	.4	10	120	8.3	2.8	15	2.2
Meniscognathus	—	—	—	—	—	—	15	2.2
Leptochamops (D)	1	.2	2	120	1.7	1.7	15	2.2
Haptosphenus (D)	1	.2	1	120	.8	.8	2	.3
Contogenys (D)	4	.6	9	130	6.9	1.7	—	—
Sauriscus	—	—	—	—	—	—	4	.6
Exostinus (C)	3	.4	8	130	6.2	2.1	4	.6
cf. Gerrhonotus	—	—	—	—	—	—	2	.3

	Bug Creek Anthills, Hell Creek Formation[4]						*Lance Formation*[3]	
	MNI	*RA*	*NS*	*ENE*	*CNS*	*RC*	*MNI*	*RA*
Pancelosaurus	15	2.1	95	130	73.1	4.9	20	2.9
Parasaniwa (C)	1	.2	3	130	2.3	2.3	36	5.2
Paraderma (D)	1	.2	2	130	1.5	1.5	2	.3
Palaeosaniwa (D)	1	.2	2	130	1.5	1.5	1	.1
Colpodontosaurus (D)	3	.4	4	130	3.1	1.0	2	.3
Litakis	—	—	—	—	—	—	1	.1
Cuttysarkus (D)	2	.3	2	130	1.5	.8	13	1.9
Coniophis (B)	1	.2	8	250	3.2	3.2	1	.1
Boidae (D)	1	.2	1	250	.4	.4	—	—
?Pterosauria	—	—	—	—	—	—	1	.1
birds (D)	1	.2	1	150	.7	.7	7	1.0
Mesodma	148	20.4	993	84	1182.1	8.0	55	8.0
Cimexomys (B)	10	1.8	50	84	6.0	1.4	—	—
Cimolodon	P	P	P	P	P	P	23	3.4
Essonodon	P	P	P	P	P	P	—	—
Glasbius	P	P	P	P	P	P	.2	.3
Cimolomys	P	P	P	P	P	P	8	1.2
Meniscoessus (C)	2	.3	4	78	5.1	2.6	11	1.6
Stygimys	28	4.0	224	84	266.7	9.5	—	—
Catopsalis	8	1.1	53	78	68.0	8.5	—	—
Didelphodon (D)	1	.2	2	108	1.9	1.9	6	.9
Alphadon (C)	3	.2	7	108	6.5	2.2	5	.7
Pediomys	2	.3	16	108	14.8	7.4	51	7.5

Gypsonictops (D)	5	.7	7	104	6.7	1.3	14	2.0
Cimolestes	P	P	P	P	P	P	5	.5
Batodon	—	—	—	—	—	—	1	.1
Telacodon	—	—	—	—	—	—	1	.1
Procerberus	11	1.6	111	104	106.7	9.7	—	—
Protungulatum	16	2.3	198	104	190.4	11.9	—	—
Totals	709	100.0	8693				687	100.0

[1] mean RC per taxon within lumped groups

[2] additions since Estes (1964: table 5)

[3] MNI and RA figures were available only for V5620; modified from Estes (1964).

[4] Only the MCZ sample was used in this calculation

Abbreviations:

MNI=minimum number of individuals
RA=relative abundance (% of total MNI)
NS=number of identified specimens of taxon
ENE=estimated number of contributing elements possible for each taxon
CNS=corrected number of specimens
RC=relative completeness of representation of skeletal elements of each taxon
—=taxon absent at locality
P=taxon present at locality but not recovered in sample used
(A)-(E)=taxa included in groups A-E in Figure 3

are noted below (pp. 21-22) with a discussion of their relevance to our study. Shotwell's terminology is used throughout this paper, and the terms are defined below (pp. 19-20).

General Comparisons

Fishes

Excepting *Squatirhina americana,* all Lance Formation sharks are present in the Bug Creek localities, although they are much rarer there. *Ischyrhiza avonicola* is represented only by a single tooth (from the Harbicht Hill locality), and *Lonchidion selachos* is represented only at Bug Creek Anthills (BCA) and by very few specimens. The best represented elasmobranch present is the ray *Myledaphus bipartitus*; this is perhaps a parallel for the fact that rays and skates are more common today in fresh waters than are other chondrichthyans. The low overall abundance of these forms at Bug Creek Anthills probably indicates a restriction of marine access relative to that of the major Lance Formation localities (Estes, et al., 1969: 28).

Bony fishes are represented by a more complete series of elements at Bug Creek Anthills than in the Lance sample; also, the state of preservation of the bone is generally better and there is less rolled and waterworn material. As a percentage of total *minimum number of individuals,* including mammals (Shotwell, 1955, etc.), bony fishes are less abundant than in the V5620 Lance sample (BCA 20%, Lance 27%). All Lance fishes also occur in the Bug Creek local faunas, and *Protoscaphirhynchus, Palaeolabrus* and *cf. Paralbula* are additional bony fish present at Bug Creek. The *cf. Paralbula* specimens do not necessarily indicate proximity of the nearshore marine environments in which this fish is usually found; more probably these few, poorly preserved specimens were transported into the Bug Creek area by some other contemporaneous animal.

In combination, the bony fishes (at least the primitive ones) indicate resemblance to the primitive fish fauna of the Mississippi River drainage today, especially in its lower reaches near the Gulf Coast (Estes, 1964: 166). *Acipenser, Polyodon, Lepisosteus,* and *Amia* all occur now in that area (See Table p. 23), as well as in the Wyoming and Montana fossil samples.

Amphibians

As for the bony fishes, the BCA salamanders show greater diversity than those of the Lance local fauna; all species found in

the latter are present and *Proamphiuma* occurs as well. Skull elements are somewhat better represented than in the Lance sample and most of the salamander bones give less indication of transportation wear. On the other hand, few limb elements of salamanders are found in the Bug Creek localities, in contrast to their relative frequency in the Lance sample. By analogy with Recent salamanders, the neotenic skull elements and vertebral form of the fossil salamanders indicate that all genera were fully aquatic (Estes, 1964), possibly excepting *Prodesmodon*.

In comparing *relative abundance* of Bug Creek species with that from the Lance Formation (Tables 1, 2; Figs. 1, 2), a significant increase for *Lisserpeton* and *Opisthotriton* is apparent, as is an equally significant and much reduced frequency of *Habrosaurus*. Although rarity of *Prodesmodon* makes comparison less meaningful, there seems to be a significant decrease in abundance. *Scapherpeton* shows an increase of a less striking magnitude. The total *relative abundance* (Table 1) of salamanders at Bug Creek Anthills (35.5%) is significantly greater than at V5620 in the Lance Formation (21.4%). The two quarries indicate great similarity in the manner of their deposition and this difference probably has ecological significance, as suggested below.

Sirenid and amphiumid salamanders resembling the fossil forms still live in the southeast United States today, while the Cretaceous frogs indicate relationships to now extinct or relict groups: discoglossids are now Palearctic and Oriental, and the Bug Creek forms show relationship to genera from both of these areas. With the possible exception of the *Alytes*-like form, all Bug Creek

TABLE 2

Comparison of *minimum number of individuals* and *relative abundance* of salamanders in two late Cretaceous localities.

	V-5620, Lance Formation		*Bug Creek Anthills, Hell Creek Formation*	
	MNI	RA	MNI	RA
Habrosaurus	71	49	9	4
Scapherpeton	22	15	61	24
Lisserpeton	1	1	72	28
Opisthotriton	41	28	107	42
Prodesmodon	11	7	2	1
Proamphiuma	0	0	2	1
	146	100%	253	100%

frogs appear to have been aquatic or semiaquatic, judging from their modern counterparts. The frogs are similar to those from the Lance Formation in being primarily discoglossid and in having genera in common (*cf. Barbourula, Scotiophryne, Eopelobates?* sp.).

Turtles

All Lance turtles identified by Estes (1964) are represented at Bug Creek, except that *Adocus* seems to have replaced its close relative *Basilemys,* and undescribed baenid 2 does not occur in the Lance local fauna.

The baenids are the most abundant of the turtles; unfortunately they have no modern relatives and their ecological requirements are unknown. Both the baenids and the emydine-like testudinid were probably amphibious-aquatic types.

The other turtles are fragmentary and poorly represented. The trionychid material indicates permanent waters, either large rivers or streams, or large quiet bodies of water with soft mud or sandy bottoms.

Champsosaurs

Champsosaurs were aquatic, fish-eating reptiles that perhaps filled niches analogous to those of the Recent gàrpike or the gavial.

Lizards

Diversity of the lizard fauna from the Bug Creek Anthills locality is about the same as in the Lance Formation. The Lance forms *Meniscognathus, Litakis, cf. Gerrhonotus,* and *Sauriscus* do not occur, but these genera are very rare in the Lance Formation localities. In comparison with the latter, *relative abundance* of lizards at Bug Creek is strikingly reduced and the material is poorly preserved. *Contogenys* replaces *Sauriscus* as the scincoid in the fauna, and the highly specialized teiid *Peneteius* makes its first appearance. Only the anguid *Pancelosaurus* (Meszoely, 1970) is as abundant as it was in the Lance sample (approximately 2-3% of total individuals represented in the sample), suggesting that it may have been amphibious or aquatic.

Snakes

The oldest known North American snake, *Coniophis* (Lance Formation, Wyoming), occurs in a number of other North American Upper Cretaceous, Paleocene, and Eocene deposits. With

the exception of *Helagras* from the Puerco and Torrejon Formations, no other fossil snake has been known to occur in North America until the Eocene.

The presence of a boid snake at Bug Creek Anthills is indicated by a single vertebra. This snake may have been related to the burrowing (or cryptic) Oligocene to Recent subfamily Erycinae.

Crocodilians

Presence of both crocodiles and alligators in the Bug Creek local fauna recalls the situation in subtropical Florida today, in which both *Alligator* and *Crocodylus* are represented. Jepsen (1963: 680) has suggested that crocodilians occupied ecological niches in the past that are filled today by large terrestrial mammalian carnivores. Analysis of stomach contents of Recent crocodilians (Kellogg, 1929) reveals that only about 6% of their food is mammalian. If Kellogg's study can be used as a criterion, it is likely that, as today, mammals did not form a significant part of the diet of crocodilians in the past. Since the primary food of large mammalian carnivores today is other mammals, the niche relationships of crocodilians and large terrestrial mammalian carnivores are not necessarily comparable. Assuming the food habits of crocodilians to be conservative, it would be more logical to assume that large mammalian carnivores (themselves preying on mammals) evolved with their prey. This assumption can be correlated with, and receives support from, the late Cretaceous and early Cenozoic appearance of the significant predators of mammals: snakes, large varanid lizards, some birds, and of course, the carnivorous mammals themselves.

Dinosaurs

Although similar in diversity to those from the Lance Formation, the dinosaurs at BCA are represented by a lower *relative weight* of specimens (see below, and Table 4). *Tyrannosaurus* is not present at BCA, and has not been found in the upper 100 feet of the Hell Creek Formation. We have used the name *Gorgosaurus* rather than *Dryptosaurus* here (*cf.* Estes, 1964) although firm generic identification cannot be made on the basis of isolated teeth. Sloan (1969, pers. comm.) states that all Hell Creek Formation ceratopsians are referable to *Triceratops prorsus,* and all hadrosaurians to *Anatosaurus copei.*

Methods of Analysis

Paleoecological analysis of any large sample of a diverse fossil vertebrate assemblage may yield useful information about past inter- and intra-community relationships, and contribute to an understanding of community development through geologic time. Such analysis must take into consideration factors that elucidate taphonomic changes (Olson, 1966) between the original community structure (life assemblage) and the death assemblage that the fossil sample represents. Some death assemblages preserved in or near their natural habitats (e.g., those of pond deposits), may differ little from their counterparts in life. Most fossil vertebrate deposits, however, result from deposition by moving water and thus may have their original composition modified by a variety of sedimentary, biological, and ecological factors. The weight differences between compact and spongy bone tissues, the size of bony elements, the amount of preservable tissue available in an individual, and the relative fragility of the skeletal tissues may interact with current speed to modify the original composition of the life assemblage. Sedimentary sorting may thus produce a sample radically different from the original life composition. Proximity of the life zone of the animals to the eventual area of deposition of the fossils is also a factor modifying the assemblage, and, as Olson points out, deposits formed by moving water may "tap a variety of life zone along the course of the stream and its tributaries."

Shotwell (1955, 1958, 1963) devised a quantitative method by which environmental reconstruction of some late Cenozoic mammal communities could be made. Many late Cenozoic vertebrate fossil samples are predominantly mammalian. This is the result of collecting bias in some samples, but other factors may apply. For instance, deossification has progressed through time in many lower vertebrates, resulting in fewer, more delicate bony elements in their descendants. Also, the relatively coarse sediments in which many late Cenozoic vertebrate samples occur imply rapid currents of deposition and a high rate of erosion of delicate elements.[1] Another factor is ecological; temperature and humidity have decreased in North America and Europe since the middle

[1] Bulk collecting methods may produce a large lower vertebrate fauna; thus Wilson (1968) collected a Pliocene fauna with 39 lower vertebrate and 34 mammalian species. Also, Shotwell (1969, *in litt.*) indicates that his recently collected samples "are primarily lower vertebrates, *at least those occurring in fine-grained sediments* [emphasis supplied]."

Cenozoic, and areas that were once humid, subtropical, and tropical are now temperate and more arid. Many lower vertebrates have retreated south in response to these changes, remaining with their temperature optima and evolving quite slowly or becoming extinct; many temperate niches thus became available for capture by the rapidly evolving mammals.

The community analysis method devised by Shotwell (1955) is summarized in his 1958 article. We will not recapitulate his method or findings here, but the major precepts of his analysis will, we hope, emerge in context below.

The first parameter obtained from a community analysis utilizing the Shotwell method is the *minimum number of individuals* (hereafter referred to as MNI). The MNI itself, reflecting the fewest number of individuals required to produce the fossil elements, is a rough indication of abundance, but it is more useful as a percent of the total MNI of the sample: this is the *relative abundance* (RA). The relative abundance alone is a ready means of comparison of samples, and one that is not difficult to calculate; Estes (1964) used it to show the constancy of vertebrate abundance in numerous Lance Formation localities. Wilson (1960: 9) suggested that a percentage "derived from numbers of specimens, with perhaps some subjective adjustment for other considerations" could be as useful as Shotwell's method. To us, percentages calculated from the actual numbers of individuals present have a clear biological advantage over those derived merely from numbers of specimens, especially for lower vertebrates. Bones of the latter are often common, particularly if an extensive dermal skeleton is present. Sedimentary or erosional factors, such as those operating postdepositionally in "blowout" accumulations, may selectively act on bones, and the number of elements, especially resistant ones, is thus much less likely to reflect actual abundance. Nevertheless, "accuracy" of the Shotwell or the Wilson method is not demonstrable for a fossil sample. Confidence in either method can only be *suggested* by the use of theoretical models or collection of material from modern sediments and comparison with existing abundance; these data are, in general, difficult to obtain and not yet available (Van Valen, 1964: 109).

As Shotwell has pointed out (1955: 331) different mammal groups vary widely in the number of elements that can be contributed by one individual. This difficulty is magnified when lower vertebrates are considered. Some species are wholly or in part cartilaginous or show strong ontogenetic variation in ossification. Others may enrich the sample (and perhaps give a false impression of abundance) by contributing mainly shed teeth from

an essentially continuous replacement process. In addition, because of the great antiquity of the fauna, some animals may contribute more bones than their Recent relatives because of decrease of ossification in, and loss of elements by, the modern forms. Therefore Shotwell's *corrected number of specimens* (CNS) (see below), a correction necessary because of group variation, is almost certainly a more variable factor as we have used it than it is for late Cenozoic mammals. We have given the *estimated number of contributing elements* (ENE) for the various taxa, basing it on the number of preservable, identifiable bones in modern relatives or in known complete fossil material. These estimates are necessarily approximations but are probably correct within the context used here. When Shotwell (1958: 273) made corrections in his 1955 figures, he noted that "the results are little different from those presented earlier," and we have made calculations with similar results. The estimates vary from animal to animal for reasons noted at the beginning of this section. Thus for the ray *Myledaphus* we include a figure only for teeth and precaudal vertebral column as the only recognizable, preservable structures, yet even this figure approaches five hundred, whereas for mammals, in which most bones are identifiable, the total figure is only about one hundred and ninety.

The total number of specimens for the species (NS) and the estimated number of elements (ENE) yields a *corrected number of specimens* (CNS) when formed as a ratio:

$$\text{CNS} = \frac{\text{number of specimens} \times 100}{\text{estimated number of elements}}$$

(Shotwell, 1958: 272-273). The *relative completeness* (RC) for each species is then determined according to Shotwell (1955: 332). This is the corrected number of elements for *each individual:*

$$\text{RC} = \frac{\text{CNS}}{\text{MNI}}$$

The RC is the parameter that is used to determine the closeness of an animal to the site of deposition and thus can be used as a measure of whether the animal belongs to a "proximal" or "distal" community (Shotwell, 1955: 330). In a wind-deflation locality ("blowout") the RC is less valid because erosion causes delicate elements to become unrecognizable in a short period of time. In such blowouts, the RC may become a measure of animals possessing the most numerous durable elements (Estes, 1964: 151-152). This is not the case with Bug Creek Anthills, however, which is a quarry.

Table 1 gives MNI, RA, NS, ENE, CNS, and RC for each species identified in the MCZ sample from Bug Creek Anthills; MNI and RA from Lance locality V5620 are included for comparison. A few rare taxa are not included since they were not recovered in the MCZ sample (*cf.* pp. 3-8).

Finally, it is necessary to discuss the criticisms of Shotwell's method offered by Voorhies (1969), in order to justify our use of it here. Voorhies discussed taphonomic processes that produced an accumulation of Pliocene vertebrate fossils in Nebraska, and emphasized the lack of sedimentary data used by Shotwell in his analysis. Shotwell assumed that attritional mortality produced the quarry accumulations in Oregon on which he developed his method; he could thereby interpret the minimum numbers of individuals as being representative of actual abundance in the Pliocene. Voorhies, on the other hand, suggested (1969: 54) that stream sorting of bones caused many of the differences between quarries that Shotwell ascribed to community differences. The fact that the Pliocene quarry accumulation in Nebraska was the result of mass mortality (probably winterkill) seems to have generated many of Voorhies' criticisms of Shotwell's method.

In spite of this and other objections raised by Voorhies, we feel that the minimum number of individuals recovered at Bug Creek Anthills and at the Lance Formation localities is, in general, representative of former life abundance. Our reasons for this belief are listed below but are specific to the localities studied here; each fossil accumulation must be judged separately. Techniques such as those proposed by Shotwell must be applied to a variety of fossil accumulations of diverse ages before the overall utility of the method for environmental reconstruction can be determined.

1. Estes (1964: 151-158) demonstrated the essentially uniform relative abundance of individuals in Lance Formation localities, and Estes et al. (1969; this paper, pp. 10-13) have shown that Lance relative abundance is similar to that at Bug Creek Anthills. In addition, the large BCA collections in various museums do not differ materially in relative abundance *inter se*.
2. The Lance and Hell Creek samples are composed of relatively small animals, in contrast to those studied by Voorhies and Shotwell. The common animals in the Cretaceous samples are represented by almost all of the principal skeletal elements. Although sedimentary sorting has modified relative numbers of some bones, their varied shapes and

sizes seem to indicate that sedimentary factors have not been the only influence on accumulation. With rare exceptions, selective preservation of uniform, durable elements (Estes, 1964: 157) does not appear to have modified relative abundance significantly either at V5620 or at BCA.

3. Abrasion of bony elements of members of the aquatic "proximal community" is significantly less than that for members of the various "distal communities." As in Voorhies' sample (1969: 57), a range of fresh and abraded examples of each bone can be demonstrated at BCA, reflecting, probably, contemporaneous reworking of channel deposits as noted by Estes (1964: 159) for the Lance Formation sample.
4. Bones of larger animals such as crocodilians, large turtles, and dinosaurs are reduced in numbers by sedimentary phenomena at BCA; the slow current speeds failed to transport the large bones. Except for baenid turtles, however, all BCA material of these groups is more abraded and fragmented than that from Lance Creek, where a similar paucity of large elements also occurred. This is one factor leading us to suggest that BCA was deposited farther from a riparian habitat than was V5620.
5. While larvae or young are poorly represented at both Lance and Bug Creek localities, a wide range of body size does occur. The greater number of small rather than of large individuals of many common species seems to indicate a natural proportion rather than a sedimentary reworking, since element size of small individuals is well below the median specimen size.
6. The large size of both Lance and Hell Creek samples reinforces the above conclusions.

Admittedly the above factors are subjective or hard to quantify. Nevertheless, they seem to suggest that attritional rather than mass mortality was operating to produce the Lance and Hell Creek samples, and that the relative abundance of fossils can be assumed to bear a reasonably close relationship to actual life abundance.

Completeness of the Sample

Shotwell (1955: 329) compared diversity of his Pliocene mammal faunas with that of the Recent fauna of the United States as a whole as well as with average figures for some Recent local faunas.

His comparison indicated a reasonable similarity in diversity and he used this as an indication that his quarry methods had sampled the Pliocene fauna rather well (about 85%, if the comparison is justified), although a better comparison might have been made with a fauna ecologically and climatically more similar to his fossil fauna, perhaps from an area in Africa. Ecological interpretation of the vertebrate fauna from the Lance Formation (Estes, 1964) applies equally well to that from the Hell Creek Formation, with some differences in detail discussed elsewhere in this paper. From both faunal and climatic standpoints, the closest modern analogue of the two fossil faunas can be found in the lower Mississippi River drainage and in similar areas on the Gulf Coast of the United States. Since the Mississippi drainage is related to the former path of some of the major epicontinental seaways in North America during the Cretaceous, the similarity of the fossil and Recent faunas is not surprising.

TABLE 3

Generic Diversity of Cretaceous and Recent Faunas*

	Lance genera	Bug Creek genera	Recent genera
chondrichthyans	4	3	3
chondrosteans	2	3	3
holosteans	4	5	2
teleosteans	3	4	34
(total fishes)	(13)	(15)	(42)
amphibians			
salamanders	5	6	10
frogs	4	4	5
(total amphibians)	(9)	(10)	(15)
reptiles			
turtles	6	7	11
eosuchians	1	1	0
lizards	14	12	5
snakes	1	2	18
crocodilians	2	2	1
dinosaurs	10	8	0
(total reptiles)	(34)	(32)	(35)
birds	5	1	149
mammals	14	16	36
total genera	75	74	277
total genera removing birds	70	73	128

*The Recent fauna is that of southeastern Louisiana, the delta region of the Mississippi River (Blair, et al., 1968; Lowery, 1960; Bishop, 1947).

Table 3 compares the number of vertebrate genera for the two Cretaceous localities with that for the Recent Mississippi drainage area in southeastern Louisiana. Birds are included, although they must be removed in the final analysis (Shotwell, 1955: 328) in order to make the results more comparable. Table 3 shows several obvious major differences from the modern fauna: (1) relative absence of teleosts, snakes, and birds, (2) presence of dinosaurs, and (3) primitive nature of the mammals. Teleosts present in the modern fauna are mainly Clupeiformes, Cypriniformes, and Perciformes. The former group is not represented at Bug Creek but was common in contemporaneous seas. They would be difficult to recognize on the basis of disarticulated remains and may occasionally have penetrated into the freshwaters of the Cretaceous as they do today. Cypriniformes are not known before the Eocene. Perciformes first occur in the Cretaceous (Estes, 1964; Estes, et al., 1969) but they are not common until the Eocene. Relative lack of diversity of these two orders in the Cretaceous samples is thus probably in part an evolutionary rather than a sampling phenomenon.

The dinosaurs contribute notably to the Cretaceous fauna but are of course absent from the Recent fauna, where their niches as large herbivores and carnivores have been filled primarily by Artiodactyla and Carnivora.

The relative absence of snakes from the Cretaceous fauna is probably of evolutionary origin; most Recent and Cenozoic snake diversity occurs within the Colubridae, a family not yet known before the Miocene.

Only one bird is known from the Bug Creek Anthills site; Brodkorb (1963) has noted the presence of five genera in the very similar Lance local fauna. Even so, the presence of approximately 150 genera of birds in the Recent fauna of southeastern Louisiana forms the greatest contrast of fossil and Recent faunas. The habits of birds and the delicacy of their bones are probably partial reasons for the relatively small number of known late Cretaceous birds. However, as Brodkorb points out (1963: 70), the known Cretaceous forms (while well-distinguished) indicate that the characters of the modern orders are merging, and again much of this discrepancy between modern and fossil fauna must be an evolutionary one.

The difference in mammalian fauna seems also to be of evolutionary origin, since the Cretaceous fauna belongs to six primitive orders. The overall discrepancies between Recent and fossil groups

are easily seen, and when the difference in evolutionary development in fishes, snakes and birds is taken into account, the fossil sample may represent as much as two-thirds of the vertebrate species that might have lived on the Cretaceous mid-continental floodplain. As Fox (1968) has noted, the diversity known in the fossil habitat does not necessarily reflect the total diversity that was actually present in a group during the late Cretaceous; other habitats not represented in the fossil record undoubtedly included related forms.

Relative Weight

Shotwell (1955, 1958, 1963) did not discuss the possibility of using figures based on weight of fossil specimens. It is clear that the vagaries of preservation and mineralization preclude using weight of fossils as an indication of biomass, however useful this item of information might be. Nevertheless, we have obtained some useful results from carefully qualified use of the relative weight (RW) of specimens for major groups of lower vertebrates and some other fossil material from both Lance and Bug Creek localities (Table 4). Specific gravity of the material and relative size of the animals from both V5620 and BCA are essentially identical; use of weight therefore seems justified.

The information on relative weight that is of particular interest is based on material that cannot be used to express the minimum number of individuals easily (if at all). For instance, floral materials are not common in washed and screened material. Seeds may occur, however, often as durable casts of the inside of the seed coat. In the Lance Formation locality V5620, such seed casts are common and may indicate closeness of that locality to streambank or riverbank, a conclusion also supported by the high relative weight of turtle material. Twice as much unidentifiable material occurs at V5711 than at V5620, emphasizing the extent of erosion in a blowout locality. The slightly higher RW of coprolites at V5711 is probably also caused by resistance to erosion of these hard pebblelike objects. At BCA, coprolites are rare, and invertebrates (except for a few traces) absent; this is probably because of deposition of the fossils farther away from the shore.

The abundance of bony fish material at BCA is clearly shown by the weight data. Although the relative abundance of Bug Creek bony fishes is slightly less overall than at Lance localities, the large amount of identifiable, unworn material at BCA makes it clear that this locality was quite close to the natural habitat of

(especially) *Lepisosteus* and *Amia*. Estimated body size of these two common fishes was similar in the two localities, so that this factor does not influence the weight data.

The difference in amount of dinosaur material is quantified by the weight data. Although tooth size of some BCA dinosaurs is slightly smaller than in the Lance localities, the difference is not enough to affect the relative weight significantly. In part, the reduction in RW of dinosaur material at Bug Creek, when compared to that of the Lance localities, may represent reduced frequency of dinosaurs in the presumed deeper, more open channels represented in this area of Hell Creek deposition. Nevertheless, the reduction in numbers of dinosaur individuals in the late Cretaceous that accompanied their eventual extinction probably was the most important factor in reduction of the relative weight of dinosaur fossils.

TABLE 4

Comparison of Relative Abundance by Weight of Major Groups in Lance Formation (Wyoming: UC Localities V5711 and V5620, AM Coll.) and Hell Creek Formation (Montana; Bug Creek Anthills, MCZ Collection)

	V5711 Relative Abundance by weight (%)	*V5620 Relative Abundance by weight (%)*	*Bug Creek Anthills Relative Abundance by weight (%)*
sharks	0.25%	0.64%	0.13%
bony fishes	4.10	6.33	39.35
salamanders	1.22	1.58	3.80
frogs	0.01	0.04	0.07
turtles	8.23	35.56	8.12
crocodiles	3.53	6.79	3.32
dinosaurs	10.90	14.56	0.70
snakes	0.01	0.00	0.01
lizards	0.18	0.04	0.46
other groups	0.05	0.90	5.58
unidentifiable material	69.61	30.24	38.60
invertebrates	0.38	0.90	0.00
coprolites	1.16	0.94	0.23
seeds	0.00	1.51	0.01
	99.02%	100.03%	100.68%

Note: Calculations do not include mammals or gar scales because no weight figures were available for the Lance material.

Community Analysis

Relative Abundance

Figures 1 and 2 and Table 5 express the relative abundance (RA) of dominant genera and major groups at BCA and Lance locality V5620.

The faunal analysis diagrams (Figs. 1, 2) also include mammals, and indicate that the increased diversity of the latter at BCA in comparison with that at V5620 is accompanied by an increased relative abundance as well: RA at V5620 = 26%; RA at BCA = 33%. Lower vertebrates show greater abundance of some species at BCA than at V5620 (Fig. 1). *Amia, Scapherpeton, Opisthotriton, Lisserpeton,* and *Pancelosaurus* together account for about 50% of the MNI at BCA; the same taxa form only 27% at V5620. In the major groups (Fig. 2), bony fishes and salamanders account for about 50% of the MNI in both localities with mammals and lizards comprising about 45% of the remainder. At BCA, the relative proportions of these four groups are different from those at V5620: salamanders and mammals (rather than fishes and lizards) are the dominant groups, totaling about 65% of the MNI. There is a substantial complementary reduction in lizards, and (to lesser degree) fishes, from V5620 to BCA.

TABLE 5

Relative Abundance of Major Groups of Lower Vertebrates in Three Late Cretaceous Localities

	Lance Formation		*Hell Creek Formation*
	V5620	*V5711*	*Bug Creek Anthills*
sharks	2	1	1
bony fishes	38	25	30
salamanders	30	49	52
frogs	3	1	2
turtles	1	1	3
lizards	23	21	8
dinosaurs	2	1	2
other	1	1	2
	100%	100%	100%

These overall differences have some ecological significance, we believe. As Estes et al. (1969) note, the Bug Creek Anthills fossils indicate deposition in more open waterways, more lowland

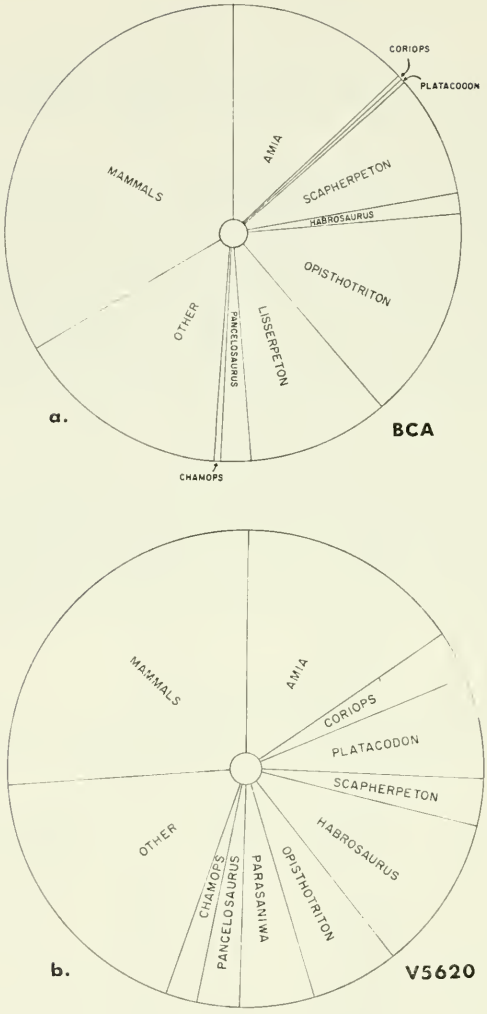

Figure 1. Relative abundance of dominant lower vertebrate genera in two late Cretaceous localities: *a*, Bug Creek Anthills; *b*, Lance locality V5620.

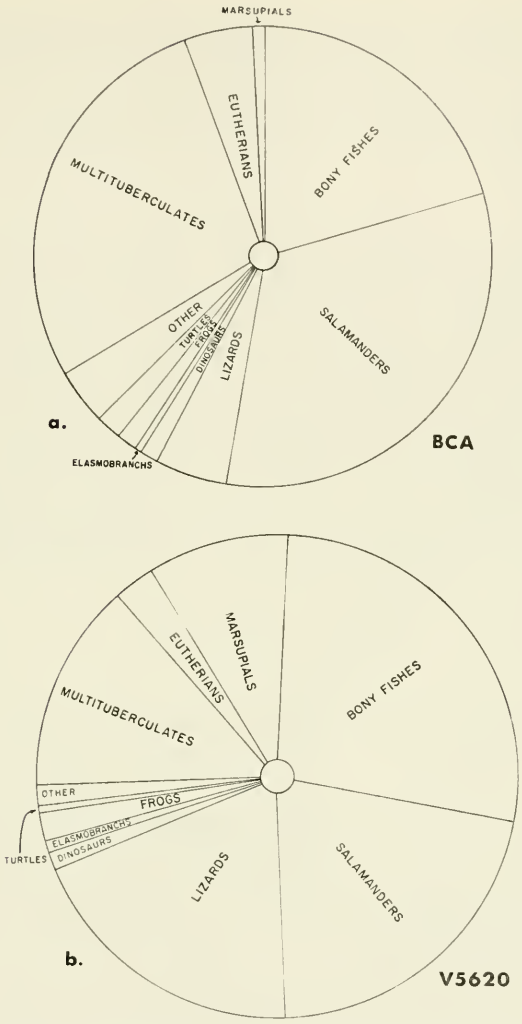

Figure 2. Relative abundance of major groups of vertebrates in two late Cretaceous localities: *a*, Bug Creek Anthills; *b*, Lance locality V5620.

habitat, and greater distance from the terrestrial, streambank habitat than do those from the Lance Formation. This difference, however, is small; the overall ecological similarity between the two local faunas, as demonstrated by the faunal list, is beyond doubt. More specific reference to the difference in habitats represented will appear below.

Relative Completeness

The relative completeness (RC) of members of the fauna was used by Shotwell (1955, etc.) to indicate proximity of taxa to the site of deposition, and by extension, he used this parameter to delimit "proximal" and "distal" communities. Shotwell (1955: 332) arbitrarily set the limit of the proximal community at the average RC (= number of specimens per individual) for the total sample. RC and RA for the Bug Creek Anthills sample is shown in Figure 3 and Table 1. At BCA this method for distinguishing proximal and distal communities does not work satisfactorily; the complexity of the fauna is not resolved by so simple a distinction. The most proximal community at BCA is, however, clearly aquatic, and includes the following dominant species:

Lepisosteus occidentalis — alligator gar
Scapherpeton tectum — aquatic (elongated?) salamander
Amia fragosa — bowfin
Opisthotriton kayi — aquatic, elongated salamander
Lisserpeton bairdi — aquatic (elongated?) salamander

Other, less common members of this aquatic community included sturgeons, the discoglossid frog *Scotiophryne,* the sirenid salamander *Habrosaurus,* the presumed amphibious lizard *Pancelosaurus,* and the baenid turtles. A proximal terrestrial (riparian) community can also be postulated to include most of the multituberculate mammals, and the two common eutherians. The high frequency of the multituberculate *Mesodma* seems to indicate that it may have overrun the soft, marshy margins of the rivers as small rodents and some other small mammals do today. *Mesodma* and the other multituberculates seem, from their dentition, to have been seed or seed-coat eaters. The primitive ungulate *Protungulatum* was probably also herbivorous, adapted for browsing on marshy vegetation. Some of the mammals may have been amphibious, as occurs today in marshy habitats in various parts of the world.

Of the total of approximately 78 species, 42 belong to the "distal community" as delimited by Shotwell's method. Considerable

taxonomic diversity occurs among the "distal" group; sharks, bony fishes, salamanders, frogs, lizards, dinosaurs, crocodilians, birds and mammals are all included. Many (rather than one) distal communities are certainly represented, some aquatic and some terrestrial. Most of the lizards, the dinosaurs (excepting *Anatosaurus*), and 13 of the 20 species of mammals probably were part of a terrestrial, streambank-riverbank community; *Coriops* and *Platacodon, Lonchidion, Champsosaurus,* and *Trionyx* seem to be the nucleus of a distal aquatic community perhaps inhabiting local ponded areas in streams, as indicated by their greater abundance in Lance Formation localities than at BCA. Amphibious species such as the emydine turtle, the dermatemydids, the crocodilians, and the remaining frogs inhabited the ecotone between aquatic and terrestrial habitats. Finally, a group of fishes of essentially marine affinities (the sharks, the elopid, *cf. Paralbula,* and *Belonostomus*) seem to represent a group of diadromous forms occasionally migrating into the major streams and rivers. Unfortunately, RC figures are not available for the Lance localities. Nevertheless, a few Lance species whose relative completeness can be subjectively

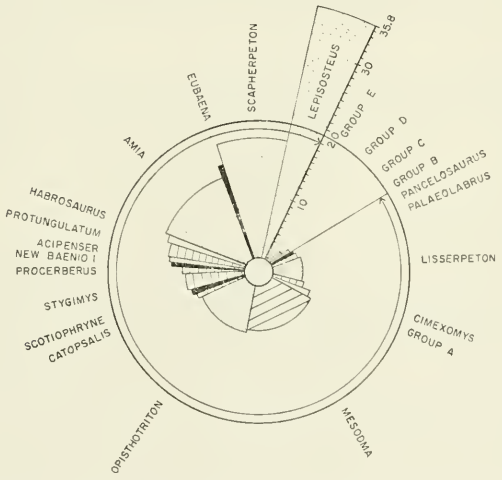

Figure 3. Relative completeness and relative abundance of vertebrates from Bug Creek Anthills. RC is given along the radius; RA in degrees of arc. The "proximal community" as indicated by the average RC (= 4.9) is delimited by the arrowed circumferential line. Members of groups A - E are indicated by letters in parentheses following the name of taxa in Table 1.

estimated reinforce some of the above conclusions. These include *Coriops, Platacodon,* and *Habrosaurus;* their apparently greater RC at V5620 than at BCA tends to confirm our suggestion (based essentially on relative abundance) that they were stream-dwellers rather than river-dwellers.

Some substantiation for the postulated habitat differences between BCA and V5620 comes from the nature of the sediments themselves. While we cannot treat this subject in detail here, the relatively greater amount of clay-sized material in the sandstone at BCA indicates more sluggish waters and deposition nearer the open areas of the waterways than was the case at V5620, where sandy streambanks appear to have been the site of deposition of the fossils.

Among recent ecological situations, Lance locality V5620 probably represents a wooded swamp habitat, with small to medium-sized watercourses and some ponding. The equivalent for Bug Creek Anthills, however, seems to be a major waterway issuing from such a wooded swamp: similar habitats were available in or near both localities, but terrestrial and riparian habitats were restricted at BCA, which may have been nearer the delta region of one of the major rivers emptying into the remnants of the late Cretaceous sea.

The flora of the Hell Creek Formation was studied by Shoemaker (1967) and Norton and Hall (1969). As for the sediments, floral analysis cannot be detailed here. However, it is worth noting that the "Transition Flora" found in the upper part of the Hell Creek Formation by Norton and Hall begins at a level slightly above that of Bug Creek Anthills, while the majority of the species of the "Upper Cretaceous Flora" disappear at a level somewhat below the locality. Floral materials are poorly represented in the sandstones of the lower half of the upper part of the Hell Creek Formation, and therefore the point at which the climatic deterioration postulated by Hall and Norton (1969) begins is difficult to determine. Similarity of the Bug Creek Anthills fauna to that of the Lance Formation, in spite of the differences in the mammalian fauna noted by Sloan and Van Valen (1965), seems to indicate that a subtropical climate (as for the Lance Formation) still prevailed in this area of Montana in Bug Creek Anthills time.

ACKNOWLEDGEMENTS

Dr. Robert E. Sloan has enthusiastically supported our efforts, and has generously allowed the Museum of Comparative Zoology to collect the fossil sample used in the quantitative study. He has also contributed much valuable information about geological setting, details of occurrence, and collecting methods. We are very grateful for his help. Mr. Arnold Lewis deserves special thanks for providing first-hand knowledge of collection of the MCZ sample. Dr. Malcolm McKenna kindly contributed the American Museum of Natural History Lance Formation sample used for comparison.

Dr. Charles Meszoely made preliminary analyses of a number of Hell Creek Formation collections from the American Museum of Natural History, University of California, University of Kansas, and Saint Paul Science Museum. These were helpful in documenting the stability of relative abundance in the MCZ collection. Mr. Berberian prepared most of the raw data and preliminary analysis of the MCZ sample.

We thank Donald Baird, W. A. Clemens, Jr., Walter Coombs, Bryan Patterson, Dale Russell, J. A. Shotwell, and R. E. Sloan for helpful suggestions.

The figures are by Mr. László Meszoly. This research was supported in part by National Science Foundation grants GB-1683, GB-4303, and GB-7176, to the senior author.

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(Received 4 December 1969.)

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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA

VI. A CHINIQUODONTID CYNODONT WITH AN INCIPIENT SQUAMOSAL-DENTARY JAW ARTICULATION

Alfred Sherwood Romer

ABSTRACT. The cranial anatomy of a small carnivorous chiniquodontid cynodont from the Middle Triassic Chañares Formation of Argentina is described and figured; this new form is named *Probainognathus jenseni*. In addition to other advanced characters, *Probainognathus* has a definite jaw articulation, accessory to that of quadrate-articular, between squamosal and dentary. It is not improbable that the Chiniquodontidae lie close to and, perhaps, on the main evolutionary line leading to mammals.

In a previous paper in this series (Romer, 1969b), I have described, as *Probelesodon lewisi*, a predaceous cynodont of the family Chiniquodontidae, and pointed out features which suggest that this Middle Triassic family, including the only known carnivorous cynodonts of that age, may well represent the therapsid line leading toward mammals. I here describe a smaller contemporary chiniquodontid which is still further advanced in the presence of an incipient squamosal-dentary jaw articulation. This form may be formally described as:

PROBAINOGNATHUS JENSENI, GEN. ET SP. NOV.

Holotype. La Plata Museum 1964-X1-14-7, a skull and jaws. Collected from the Chañares Formation in La Rioja Province, Argentina, about 3 km north of the point where the Rio Chañares debouches into the Campo de Talampaya.

Combined generic and specific characters. A small chiniquodontid cynodont, mature specimens having an average basal skull length of about 71 mm. Seven cheek teeth of the type common in carnivorous cynodonts, the cheek teeth generally showing marked evidence of wear. The squamosal has a shallow but well-defined cavity for dentary and surangular articulation.

The generic name has reference to the advanced nature of the jaw articulation. The specific name is in honor of James A. Jensen, formerly of the Harvard staff, and now in charge of geologic and paleontologic collections at Brigham Young University; he served brilliantly as a collector on both Harvard expeditions to Argentina.

Collection and preparation of this and other Chañares materials were supported by National Science Foundation grants GB-4615 and 8171.

The skull of this small carnivore (Figs. 1-3, 5, 6) is similar in nearly all regards to that of other members of the Middle Triassic family Chiniquodontidae, including the contemporary, newly described genus *Probelesodon*. Since I have described the skull of that form in some detail, *Probainognathus* may be somewhat more briefly treated by comparison with it.

The size is relatively small; the average skull length (measured from the base of the premaxillary tooth border to the condyles) is, in a series of twelve skulls, 71 mm. The skull proportions are those of chiniquodonts in general, inherited presumably from the Thrinaxodontidae. The skull is proportionately broad, with a narrow and relatively short face and a greatly expanded zygomatic region. The width across the zygomatic arches in *Probelesodon* is about 75 per cent of skull length, here nearly 80 per cent. A proportionate difference from *Probelesodon* lies in the deeper otico-occipital region, mainly related to greater depth of the parietals, and a higher occipital crest. In correlation with smaller size, the orbits are relatively larger (by about 20 per cent) than in *Probelesodon*; they appear to be directed somewhat more dorsally than in that genus. In *Probelesodon* the centers of the orbits are somewhat back of the half-length of the skull; here they are somewhat anterior to this point. As in other chiniquodontids, there is a nubbin of bone projecting into the orbit from its anterior edge external to the opening of the lacrimal duct. The sagittal crest extends further posteriorly than in *Probelesodon* before cleaving into the paired occipital crests, giving a straighter posterior margin to the skull, as seen in dorsal view, and making the occipital region below the crests more concave. The braincase is relatively broader in the parietal region.

The general pattern of the dermal roofing elements (Figs. 1, 2) is similar to that in other chiniquodonts. The snout, as in other members of the family, projects well forward of the premaxillary tooth row; the processes of the premaxillae, ascending over the

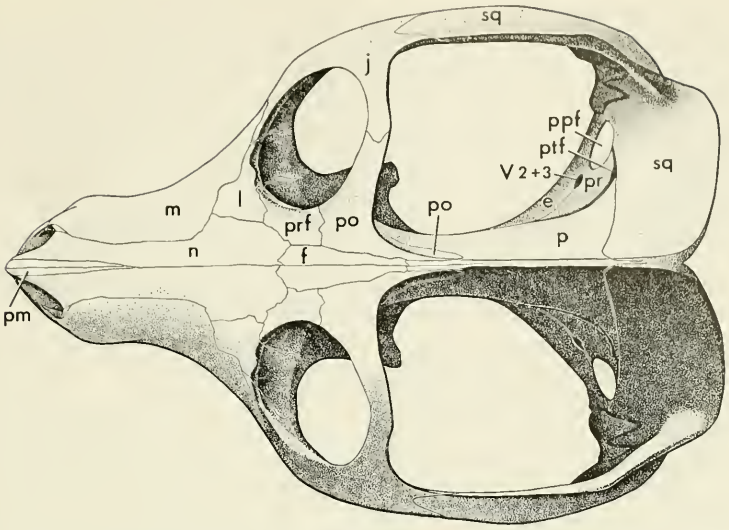

Fig. 1. Dorsal view of the skull of *Probainognathus*. This and Figs. 2-3, 5-8 are composites, about the size of the holotype. Abbreviations for Figs. 1-3 and 5-8: *a*, articular; *an*, angular; *bo*, basioccipital; *bs*, basisphenoid and parasphenoid; *c*, coronoid; *d*, dentary; *e*, epipterygoid; *f*, frontal; *fo*, fenestra ovalis; *i*, jugal; *jf*, jugular foramen; *l*, lacrimal; *m*, maxilla; *n*, nasal; *oc*, occipital complex; *p*, parietal; *pap*, paroccipital process; *pl*, palatine; *pm*, premaxilla; *po*, postorbital; *pp*, postparietal; *ppf*, pterygoparoccipital foramen; *pr*, prootic; *pra*, prearticular; *prf*, prefrontal; *pt*, pterygoid; *ptf*, posttemporal fenestra; *q*, quadrate plus quadratojugal; *sa*, surangular; *sm*, septomaxilla; *sp*, splenial; *sq*, squamosal; *st*, stapes; *t*, tabular; *v*, vomer; V_{2+3}, foramen for trigeminal nerve.

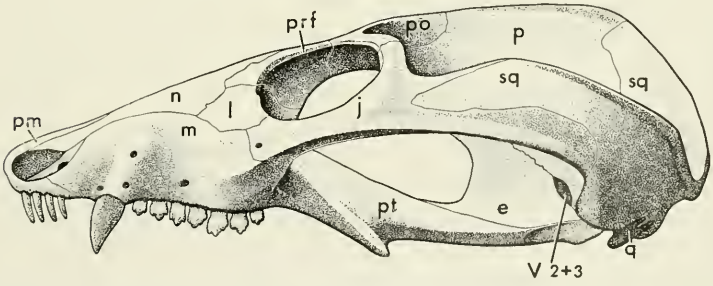

Fig. 2. Lateral view of the *Probainognathus* skull.

external nares to be inserted posteriorly between the nasals, are so slender that the snout region has been broken off in many of the specimens. With snout loss, there is little available evidence as to the development of the septomaxilla. In the Brazilian chiniquodontids (Romer, 1969a), this element is highly developed; here the only remains preserved consist of a thin layer of bone lying along the posteroventral margin of the external nares, separated in part from the maxilla by a small foramen.

The maxilla is slightly swollen in the area overlying the root of the canine, but this swelling is much less marked than in *Probelesodon.* The suborbital arch swings upward from the line of the tooth-row much more markedly than in *Probelesodon,* in correlation with the more upward facing of the orbit here. The suborbital, postorbital, and zygomatic arch regions are similar to those in other chiniquodontids except that (partially in correlation with occipital depth) the zygomatic arch swings down posteriorly more sharply than is generally the case; notable is a marked ventral extension of the squamosal at the posterior end of the arch. As in other chiniquodontids, the channel in the squamosal believed to be for the external auditory meatus is less developed than in cynognathids and gomphodonts generally.

As in other chiniquodonts, the palatine participates to a prominent degree in the formation of the secondary palate (Fig. 3), extending back in this structure to the level of the back end of the tooth-row. Since, however, the tooth-row is here relatively short, the palatine contributes somewhat less than half the length of the secondary palate, whereas, in *Probelesodon* the palatine portion is somewhat longer than that contributed by the maxillae. The two tooth-rows curve only slightly outward posteriorly, in contrast with a much greater lateral curvature in *Probelesodon,* and hence the palate is relatively narrow. In correlation, presumably, with this constriction, the outer margins of the palatal surface, just inside the posterior cheek-teeth on the maxillae, are somewhat excavated to give room for the posterior lower molars when the jaws are closed. Beneath the secondary palate posteriorly, the roof of the primary palate is more highly arched than in *Probelesodon.* As in other chiniquodontids, the palatines send posteriorly long slender processes along ridges converging backward from either lateral margin of the secondary palate. Presumably a small ectopterygoid was present, but I have not been able to determine its boundaries satisfactorily. The posterior end of the vomer is visible above and posterior to the end of the secondary palate. Pterygoid flanges are

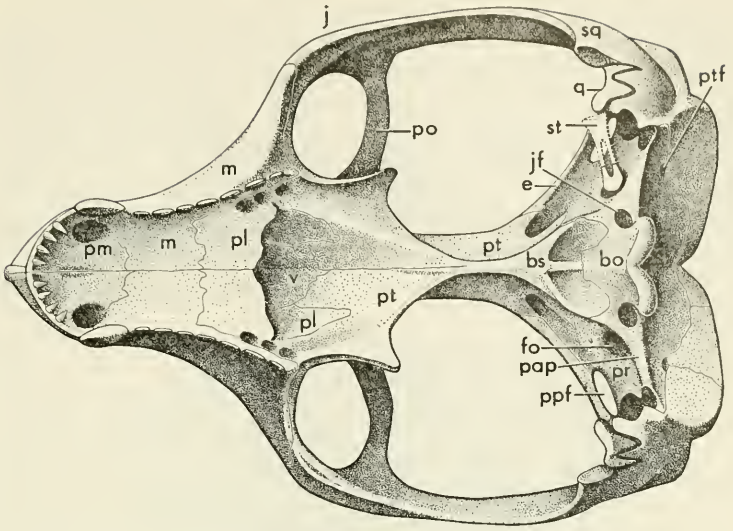

Fig. 3. Palatal view of the *Probainognathus* skull.

well developed, but are not as elongate as in *Probelesodon*. Posterior to these flanges the two pterygoids constrict and embrace the base of the braincase for some distance, as well as running out for a short distance along the flange of the palatal structure extending to the quadrate region. The main substance of this flange, however, is formed by the epipterygoid.

The general region of the jaw articulation is of interest (Fig. 4). The stapes is absent in most specimens. In one, the basal portion is still present, inserted in the fenestra ovalis. The shape of the part preserved indicates that this ossicle was rather surely of the type seen in cynodonts generally, essentially a slender quadrilateral, with a large foramen, extending out to a contact with the quadrate. The squamosal, as in other chiniquodontids and in thrinaxodontids, is distinctly divided into two rami, occipital and zygomatic, with a narrow neck between the two. The occipital ramus forms the outer side of the posterior end of the sagittal crest and descends along the anterior surface of the occipital crest. Near the point of union of the two rami are two deep notches for the quadrate and quadratojugal. In other described chiniquodonts, these notches are visible only ventrally; here, they are open dorsally as well, making the quadrate even freer than is usual in cynodonts. The

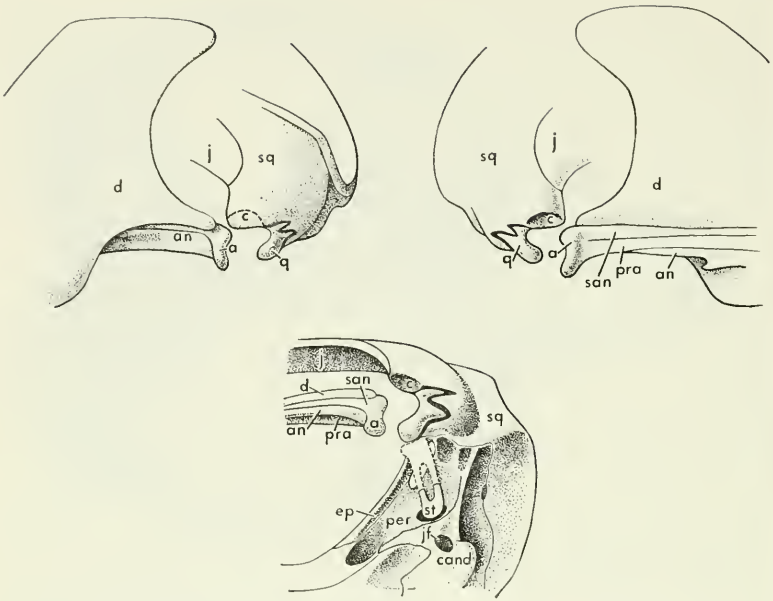

Fig. 4. External, internal, and ventral views of the region of the jaw articulation of *Probainognathus; a,* articular; *an,* angular; *c,* incipient "glenoid fossa" on squamosal; *cond,* occipital condyle; *ep,* epipterygoid; *j,* jugal; *jf,* jugular foramen; *per,* periotic; *pra,* prearticular; *q,* quadrate; *san,* surangular; *sq,* squamosal; *st,* stapes.

quadrate (with which a small quadratojugal is united), is inserted in these two notches; it is, in our specimens, always loosened and pulled anteriorly somewhat out of position, and has been lost in a number of cases. The articular face of the quadrate is convex; that of the quadratojugal is concave, apparently for reception of the projecting posterior end of the surangular. Just anterior and dorsal to the quadrate is the lower end of the pronounced ventral flange of the zygomatic ramus of the squamosal. On its inner surface, close to the anterior end of the notch for the quadratojugal, there is a shallow but well-outlined oval socket, obviously for an additional area of lower jaw articulation. The nature of this articulation is discussed below.

The anterior portion of the braincase proper has not been explored. (I hope at a later date to serial-section a skull of this form.) There is, as in cynodonts generally (Fig. 5), a large area

opposite the orbit in which the braincase wall is unossified. Posterior to this, as in other advanced cynodonts, there is an expanded epipterygoid which, ventrally, sends an extension back to a quadrate contact. As noted earlier, the parietals are somewhat greater in vertical extent than in *Probelesodon,* and slightly more expanded transversely. The basicranial and periotic regions are quite similar to those seen in *Probelesodon.* However, in several specimens the outer end of the paroccipital process is incompletely ossified, leaving a gap of somewhat variable shape and proportions between the process and the buttress formed laterally to it by the squamosal.

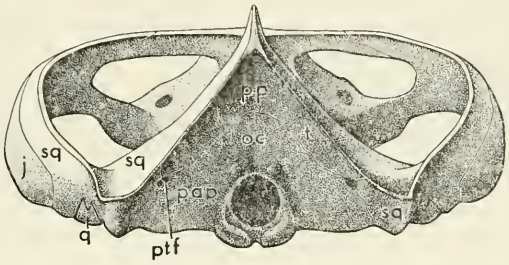

Fig. 5. Occipital view of the *Probainognathus* skull.

On the occiput (Fig. 5), the unusual posterior extent of the sagittal crest has resulted in the upper part of the occipital face of the skull being rather more concave than in *Probelesodon.* Sutures between tabulars and postparietal with the fused occipital elements are difficult to determine. The posttemporal fenestrae are small.

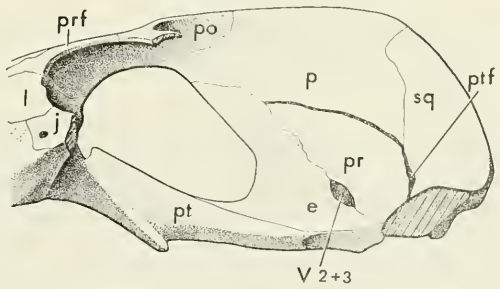

Fig. 6. Lateral view of the braincase region of *Probainognathus*; the zygomatic arch removed.

The lower jaw (Figs. 7-8) is, in general, quite similar to that described for *Probelesodon*. The dentary is very large. There is a high coronoid process, thickened along its anterior margin, which rises, in the position of jaw occlusion, nearly to the level of the sagittal crest and curves backward above nearly to the level of the jaw articulation. From the tip of this process, the posterior margin of the dentary curves forward and downward to extend posteriorly toward the articular area. This posterior projection of the dentary is little thickened, and there is no expansion in the form of a condyle. This process is incompletely preserved in most specimens, and the relation of the dentary to the other jaw bones posteriorly is frequently obscure. In the better preserved specimens, however, it seems clear that this posterior process was applied to the dorsolateral surface of the surangular, terminating just short of the posterior articular expansion of the latter bone. From its relative position, it is clear that the terminus of the dentary, together with the surangular, fitted into the shallow cavity on the squamosal external to it, and that we have here the first step in the development of the future mammalian squamosal-dentary jaw articulation.

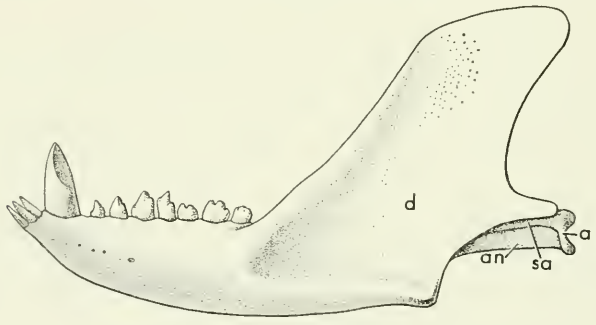

Fig. 7. Lateral view of the jaw of *Probainognathus*.

The jaw symphysis, formed almost entirely by the dentary, is a broadly fused one. Behind the symphysis the lower margin of the dentary extends backward in a nearly straight line to a sharply marked angle. This lower dentary margin is considerably thickened, with a rounded ventral margin. From the angle, the posterior margin turns nearly vertically upward and then curves backward, leaving the posterior part of the angular and, to some degree, the surangular exposed externally below it. About opposite the

posterior end of the tooth-row the dentary develops on its inner surface a horizontal ridge which extends back to the posterior end of the bone; below this thickened ridge is a lengthwise excavation in which is lodged the longitudinal "rod" of conjoined bones which support the articular.

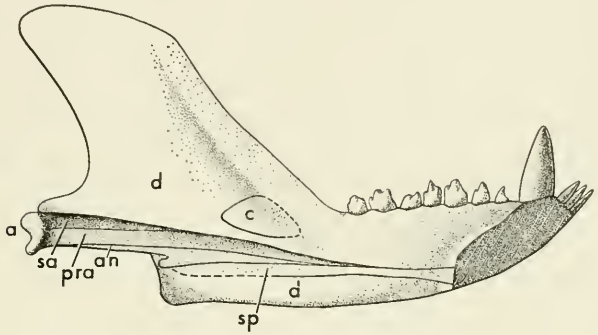

Fig. 8. Medial view of the jaw of *Probainognathus.*

The splenial is a long, but thin and slender, element. At its anterior end it takes a small part in the jaw symphysis; it is generally imperfectly preserved, but appears to continue backward, below the anterior end of the angular, to terminate at a point above the angle of the dentary. In other chiniquodontid genera I have found no trace of a coronoid bone, although it surely existed in vestigial form as a thin internal flake of bone. In *Probainognathus,* as well, it is absent in most instances. In one specimen, however, the bone is present, but is imperfectly seen (the jaws are in tight occlusion), and I am not sure of its precise outline. As in cynodonts generally, its function seems to be the provision of a surface (presumably covered with stout epithelium) to play against the ventral process of the pterygoid during jaw movement.

Disregarding for the moment the incipient dentary-squamosal contact, articulation with the skull is mediated by a moderately expanded area at the posterior tip of the jaw, which is convex dorsally where it fits into the concavity of the quadratojugal, somewhat concave ventrally to meet the quadrate proper. The lower portion of this articular area is presumably formed by the articular bone. Despite the absence of a suture, it is probable that the upper part of the articulation is formed by the posterior end of the surangular,

thus continuing to this advanced stage the quadratojugal-surangular articulation seen in various more primitive reptiles, and even in labyrinthodonts.

The functioning of this relatively small articular structure as a jaw support would be impossible were it not firmly bound to the "rod" of bone mentioned above, which runs forward more than half the jaw length in the longitudinal recess in the dentary. This structure consists of angular, surangular, and prearticular, all apparently firmly joined together and, in the case of surangular and prearticular, united without suture to the articular. The reflected flange of the angular, already small in other advanced cynodonts, is here reduced to a tiny process preserved in only one specimen; it lies far forward of the articular region, above the angle of the dentary.

As in other chiniquodontids, there are four upper and three lower incisors in each ramus; these are slender, and subcircular in section. The upper incisors are essentially vertical in position; the lowers are mildly procumbent. Canines are moderately developed; as preserved they are nearly straight, not sharply tipped, and are relatively broader anteroposteriorly than in transverse section. There are seven cheek teeth (Fig. 9) above and below in all well-preserved specimens. Their pattern appears to be that common in all carnivorous cynodonts — thin from side to side, but elongate

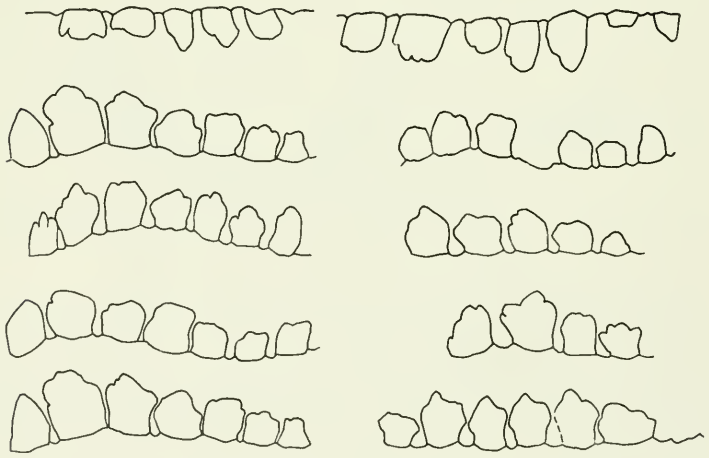

Fig. 9. Cheek teeth (shown as of the left side) as preserved in various specimens of *Probainognathus*. First four rows, upper teeth; bottom row, lower teeth, ×2½.

anteroposteriorly, with a prominent cusp at about midlength and two or three accessory cusps anterior and posterior to it. Since in most cases the lower jaws, when preserved, are in occlusion, little can be seen of the lower cheek teeth but, as far as can be observed, they appear to be similar to the uppers. A number of cheek dentitions are shown in Figure 9. It appears probable that in all cheek teeth there is, as usual in cynodonts, an accessory cusp both anterior and posterior to the principal one; in addition, however, there appears to have been a second posterior cusp in most cases. However, accurate description of the cusp pattern is made difficult because of a condition unusual in cynodonts. In most specimens, the teeth show evidence of heavy wear, leaving the tooth with a chisel-like distal shearing edge. Mr. Vincent Maglio has kindly X-rayed the upper cheek-tooth region in one specimen. As is the case, where known, in other cynodonts, all the teeth are persistently single-rooted. I have made no attempt to study tooth succession.

DISCUSSION

Probainognathus is obviously a member of the family Chiniquodontidae, resembling the other described members of this Middle Triassic group — *Chiniquodon, Belesodon, Probelesodon* — in major cranial characters. As I have recently pointed out (Romer, 1969a), the chiniquodontids are quite generalized cynodonts, readily derivable from the thrinaxodontids of the early Triassic, but more advanced in certain features. Most notable of these is the high development of the secondary palate to an essentially mammalian stage, this structure extending back to the level of the posterior end of the maxillary tooth-row, with a considerable involvement of the palatine. Further, as I have commented in discussion of *Probelesodon,* the dentary in chiniquodontids, in general, extends backward to such a degree that it must have been functionally involved in jaw articulation, although in previously described genera there was no contact of this bone with the squamosal.

Probainognathus differs from the contemporary *Probelesodon* in certain regards. It is much smaller in size. The cheek tooth-row is shorter (and, in correlation, the involvement of the palatine bone in the formation of the secondary palate is less). In the dentition, the "molars" tend to develop a fourth posterior member of the linear series of cusps. Uniquely, there is a strong trend for the wearing down of the cheek teeth to a chisel edge, with obliteration of the cusps.

Most important of differences, however, in *Probainognathus* is the development of a definite, if slight, articulation of dentary with squamosal. As described above, the latter bone curved very sharply downward over the region of the jaw articulation, and on its inner surface here shows a shallow but definitely outlined cup for articulation with the posterior end of the dentary. There is no development of a condyle of mammalian type on the dentary; the articular surface is merely the flat outer surface of the slender posterior extremity of the bone, slightly thickened in a ridge above the bar of bone (angular and surangular and prearticular) which braces the articular anteriorly. This dentary process would be too weak to be of functional significance were it not closely applied and supported by the underlying surangular.

In advanced therapsids generally, we see stages in which the dentary has increased to become the major jaw element, carrying not merely the dentition but also most of the jaw musculature. The jaw is, however, inefficient in that the dentary itself takes no part in articulation with the skull, and must rely on reduced posterior elements of the jaw to connect the dentary with the articular which, in turn, is connected with the major skull structure only through the feeble quadrate. An improved connection between dentary and skull would be highly desirable. Dr. A. W. Crompton has pointed out to me a primitive "essay" toward remedying this situation. In *Trirhachodon* (in which the dentary does not reach as far back as in chiniquodontids) there is a distinctive boss on the ventral border of the squamosal in the region of the jaw articulation. This lies close to the posterodorsal margin of the surangular (here still a fairly stout bone), thus supplementing the rather feeble articular-quadrate jaw joint (Crompton, 1963). A similar squamosal boss is present in the traversodont *Massetognathus,* and presumably performs a similar strengthening function. In the long run, however, the type of shift in the articulation initiated in *Probainognathus* was to be of much greater phylogenetic importance.

Most diagnostic criteria by which reptiles and mammals may be contrasted have to do with matters of function, or of "soft anatomy." One major osteological differentiation, useful to the paleontologist, has to do with jaw articulation. In reptiles, the joint lies between quadrate and articular; in mammals, a new joint has developed between squamosal and dentary, with subsequent loss from the lower jaw of the half-dozen elements (apart from the dentary) which were primitively present — some lost entirely, others incorporated into the middle ear.

Until recent years the reptile-mammal contrast in jaw articulation was clear-cut paleontologically. Early Mesozoic mammals are, for the most part, very inadequately known; but, in many cases, lower jaws are present in which the dentary bears a condyle indicating the presence of a squamosal-dentary articulation. And while, on the reptilian side of the picture, dentary and squamosal may closely approach one another, no actual contact between the two has previously been reported in cynodonts — the group from which most, if not all, mammals appear to have originated.

In the last dozen years or so the situation had become somewhat clouded. In some early mammals certain of the "supernumerary" jaw elements appear to have survived in reduced fashion, and in at least some early forms, notably docodontids, a quadrate-articular connection persisted accessory to a major squamosal-dentary joint (Kermack and Mussett, 1958a,b; Kermack, 1965). Crompton (1958, 1963) described, as *Diarthrognathus* a small late Triassic form of uncertain phylogenetic position (probably an aberrant offshoot from primitive cynodonts) which surely has nothing to do with mammal origins, but has paralleled the mammals in having acquired a contact of squamosal and dentary.

These discoveries resulted in a plethora of literature concerning the origin, nature, and systematics of the Mammalia which I need not discuss in detail. Currently, ideas of polyphyletic origins of groups are highly fashionable. In early mammals, dentitions and dentary bones (which generally are all the material available) show considerable variation, and it has been suggested that mammals took origin from reptiles in anywhere from four to (improbably) nine discrete lines (Simpson, 1959). Under such hypotheses the class Mammalia is not a natural assemblage — "a grade, not a clade" — and if it is attempted to restore phyletic unity to the group, it might be necessary either to restrict the class to the higher mammals, the Theria, whose unity not even the most ardent of polyphyletic advocates have (as yet) questioned, or, at the other extreme, to extend the term Mammalia downward to include part or all of the Therapsida, or even the entire subclass Synapsida.

I see no reason to adopt either of these extremes and, further, am skeptical as to whether any major degree of polyphyly is involved in mammal origin. It is axiomatic that if all stages in the evolution of one group from another were known, it would be impossible to make a definitive separation between the two. In attempting to draw a line between reptiles and mammals, all the changes involved should be considered, rather than using a single feature as

arbitrarily definitive. If, for example, we were to define a mammal (as frequently advocated) as a form in which an articulation between squamosal and dentary had been attained, *Probainognathus* would be, necessarily, separated from its obvious close relatives in the family Chiniquodontidae and removed, not merely to another family or order, but to an entirely different class of vertebrates! This would be absurd. The reptile-mammal boundary should be established not on a single character, but on a consideration of the sum total of the features by which a fully developed mammalian type is distinguished from its reptilian forebears (Simpson, 1959; Romer, 1965). Far more important than initiation of a shift in jaw articulation are changes in: cheek-tooth succession (and roots); the auditory region; and, most especially, growth of the brain to mammalian pattern and size, with concomitant reorganization of braincase structure. If (as one may hope) adequate knowledge of cynodonts and primitive mammals of the late Triassic presently becomes available, the next generation of research workers will surely be troubled in establishing a boundary; happily for us today, the gaps in our knowledge are such that we can maintain the position that all well-known therapsids lie definitely below a proper point of class cleavage.

As said above, I see little reason to believe that there has been any great degree of polyphyly in mammalian origins (except possibly in the case of a few groups in which dental evidence is obscure: monotremes, multituberculates, and the problematical little haramyids). If we survey the Reptilia for mammal ancestors it seems clear that these ancestors lie among the theriodont therapsids. Further, as far as our present rather considerable knowledge of theriodonts goes, it is only to the carnivorous Cynodontia that we can turn with confidence for mammalian forebears. Among the Mesozoic mammals, we find interesting differences in cusp patterns in the cheek teeth and in the presence or absence of an angle on the dentary; but there is, as yet, nothing known of these groups which would debar derivation of most if not all of them from typical cynodonts with an enlarged dentary and cheek teeth with a simple fore-and-aft pattern of cusps. We need not claim that all mammals have descended from a single species of advanced cynodont; but there need not, I think, have been any notable degree of polyphyly concerned.

Cynodont cranial-structure has often been compared, with profit, with that of mammals. Such comparisons have been based, of necessity, on the structure of Lower Triassic cynodonts, in default

of any adequate knowledge of later types. With accumulating knowledge of the Middle Triassic family Chiniquodontidae, such comparisons may now be made starting from a somewhat more advanced cynodont level. A major difficulty in any study of this sort lies in the fact that because of our inadequate knowledge of cranial structure of early mammals, our comparisons are in general made, compulsorily, with advanced therian types. We are now aware that many early mammals still retained traces of the reptilian pattern in jaw structure, and the same was surely true of the skull as well. It is to be hoped that work on Triassic mammal material now in hand, but not as yet described, will yield data of interest in transitional features.

Surely the greatest advance made by mammals over their reptilian ancestors lies in the reorganization and enlargement of the brain, with a necessarily concomitant restructuring of the brain cavity. Some degree of change in this area appears to have been occurring among cynodonts, as is seen in the olfactory bulb-turbinal arrangement in *Diademodon* and *Nythosaurus* (Watson, 1913). But even in chiniquodontids there is little evidence of advance in brain size. As in other cynodonts, the endocranial cavity was still small. The epipterygoid is already expanded as an alisphenoid, but the involvement, as seen in therian mammals, of orbitosphenoid and frontal in the sheathing of the expanded brain, was still to come. It is reasonable to believe that mammalian brain evolution progressed slowly during the course of the Mesozoic, and when adequate material becomes available one may expect that mammals of the late Triassic (and even Jurassic) may show a brain much less expanded, and perhaps less perfectly ensheathed in bone than in Cretaceous and later therians (Simpson, 1927).

The otic region is one in which change has been initiated in chiniquodontids, but is far from completed. It is reasonable to believe that the eardrum lay close to the region of the jaw articulation in cynodonts (Parrington, 1955). The stapes is in proper position and, presumably, in contact with the quadrate. This element (with the conjoined vestige of the quadratojugal) is already small in size and (as shown by its frequent loss in specimens) is but loosely socketed in the squamosal, and seems readily available for transformation into an incus once the shift in the jaw joint had occurred. The articular, as the future malleus, is also small in size and, of course, in proper articulation with the "incus," i.e., quadrate. Here, however, a considerable change must be made to

reach mammalian conditions, for closely connected with the articular is a bar of bone formed by prearticular, surangular, and angular (without which the cynodont articular would be ineffective in jaw articulation). This structure could not be reduced until the new dentary-squamosal joint was well established. As the evidence of marsupials and early placentals shows, construction of an auditory bulla for ossicle protection and tympanum support was a late and variable development. There is a puzzling point here. The entotympanic is a mammalian neomorph, but the Y-shaped embryonic tympanic bone of marsupials has been not unreasonably compared with the reptilian angular, one branch of the Y thought comparable to the reflected lamina of the therapsid angular (Watson, 1951, fig. 67, etc.). However, in advanced cynodonts this lamina has been reduced almost to the vanishing point and lies far forward from the presumed position of the eardrum.

The replacement of the old jaw articulation by the new has always been assumed to have been a gradual process rather than a "great leap forward," and the condition in *Probainognathus* is in agreement with this assumption. In advanced cynodonts generally, and in chiniquodontids especially, the dentary has enlarged to assume much of its future mammalian size and pattern; and, as I have earlier noted (Romer, 1969b), in chiniquodontids generally, it is so close to the squamosal near the region of the reptilian articulation that it was surely a functional element in jaw suspension. In *Probainognathus,* actual articulation is initiated; further development of a glenoid socket and expansion of the posterior tip of the dentary to condylar form during the early stages of mammalian development can be readily envisaged.

In still other regards than those mentioned, the chiniquodontid skull can be rather closely compared with that of a generalized mammal. A number of changes in dermal bone pattern are needed to attain advanced, therian, mammalian structure; it is to be expected that certain reptilian features were retained in the skull of early mammals. In the narial region the ascending internarial processes of the premaxillae (already very slender in *Probainognathus*) disappear in mammals while, on the other hand, the premaxillae push upward back of the nares, with elimination of the septomaxillae. The maxilla, already enlarged in cynodonts, pushes farther backward and upward, with reduction of its neighbors and elimination of the prefrontal. The postorbital bar, already slender in chiniquodontids, disappears with elimination of the postorbital

element. The parietal foramen, much reduced in cynodonts generally, has disappeared in chiniquodontids. In this family the sagittal and occipital crests already have the mammalian pattern, as does the occiput. The condyles are of the double, mammalian type; the four occipital elements are already fused in mammalian fashion, and the postparietal and tabulars, which have united with the occipital bone in mammals, are at least partially fused with it in chiniquodonts. In the palatal surface, the anterior region is already close to the mammalian condition in chiniquodontids. The secondary palate is already developed to mammalian status. Further palatal changes required are: elimination of the ectopterygoid, already quite small in chiniquodontids; reduction of the extent of the pterygoid posteriorly; and reduction (with elimination of the quadrate-articular jaw joint) of the posterior extension of the epipterygoid toward the articular region.

In sum, apart from expansion and elaboration of the brain capsule and changes (already initiated in chiniquodontids) in the auditory and jaw joint region, modifications needed to transform a chiniquodontid skull into that of a primitive mammal are not too numerous and not of major magnitude. I see nothing in the structural pattern of such a form as *Probainognathus* which need debar it from a position directly antecedent to a primitive mammal. At present, chiniquodontids are known only from South America, but it is not improbable that they will be found in the future to have a wider distribution. It is not unreasonable to believe that in this family we have a group of direct mammalian ancestors.

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(Received 3 December, 1969.)

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LOWER TRIASSIC (SCYTHIAN) AMMONOIDS FROM NEPAL

Bernhard Kummel

ABSTRACT: The Austrian Dhaula Himal Expedition to Nepal of 1963 reported a thin unit of limestone of Lower Triassic (Scythian) age conformable on Late Permian limestone. The Triassic units contain two ammonoid faunas, the lower comparable to the *"Meekoceras"* beds of the Himalayas and the second, containing *Anasibirites,* is of mid-Scythian age. The lowest of these faunas is separated from fossiliferous Permian beds by one meter of unfossiliferous limestone.

As a member of the Austrian Dhaula Himal Expedition of 1963, sponsored by the Austrian Himalayan Society, Dr. Gerhard Fuchs (1964, 1967, 1968) studied and mapped a large area of the Nepal Himalayas in the region of Dhaulagiri. An interesting result of this study was the discovery of late Permian and early Triassic strata in apparent conformity. Fuchs (1967: 18) summarized the character of the Lower Triassic strata as follows: "The Lower Trias forms a thin (10-25 m) easily recognizable band. At the base there is a bed of dark limestone 1.5-2.5 m thick with ferruginous weathering. The lowermost part of this bed is still Permian [Collection 108] 0-0.8 m above base, while in the upper part the first ammonites are found 1.5-2.5 m above base. Grey shales with a few limestone layers, then light, thin-bedded, dense limestones and dark nodular limestone succeed.

"In the northern parts of Dolpo the basal bed is rich in Fe and Mn showing a violet to brown colour. Here ammonites are the only fossils while in the S also lamellibranchiata are found. The fauna as well as the character of the sediments indicate bathyal or even abyssal deposition, showing that the sea had deepened rapidly at the beginning of the Mesozoic. The Lower Trias of Nepal is similar to Painkhanda and Spiti, but differs from eastern Kumaon. The latter seems to have been deposited near the southern shore of the Tethys."

In June, 1967, I was able to examine in Vienna Dr. Fuchs' collections from these Lower Triassic formations. The preservation is in general very bad and most specimens are distorted and elliptical in shape. From this assemblage the best preserved specimens of five collections were made available for study. A summary of the locality and horizon data on these collections is given in Table 1.

TABLE 1

Fossil localities of Lower Triassic of Nepal

Collection Number	*Description*
106	Five meters of light gray and blue-gray, platy limestone 14 meters above last bed with Permian fauna. At Kar, 3.7 kilometers WNW of Tukot (Barbung Khola).
107	A two-meter bed of thin platy, light gray limestone directly overlying highest fossiliferous Permian limestone in same section as collection 106.
96	3.5 meters of gray platy limestone 17.2 meters above last bed with Permian fauna. Upper course of the valley E of Terang (Barbung Khola).
95	Two meters of light gray, platy-layered limestone one meter above last bed with Permian fauna, same section as collection 96.
110	Seven meters of platy limestone with gray, clay-slate interbeds, upper Scythian, 4.3 m above base of measured section. 6 km N of Barbung village on the N running ridge (Barbung Khola W side).

Two distinct Scythian ammonoid zones are represented in these Nepal faunas. The uppermost, represented by collections 106 and 110, belong to the *Anasibirites* Subzone of the *Owenites* Zone and is mid-Scythian in age. Collection 106 contains only *Anasibirites kingianus*. Collection 110 contains *Anasibirites kingianus* and *Hemiprionites typus*. Both these genera are very characteristic of the *Anasibirites* Subzone. Faunas of this subzone are known from Kotal-e-Tera, Afghanistan (Kummel and Erben, 1968), the Upper Ceratite limestone of the Salt Range (Waagen, 1895; Kummel, 1966), from Byans in the Himalayas (v. Krafft and Diener,

1909), from Timor (Welter, 1922), South China (Chao, 1959), western Australia (identified on basis of photographs sent by B. E. Balme), from Japan (data summarized by Bando, 1964a), Primorye region (Zakharov, 1968), and western United States (Mathews, 1929; Smith, 1932; Kummel, 1954).

The second Scythian horizon is that represented by collections 95, 96, and 107 and is summarized as follows:

Collection 95
"Ophiceras" cf. *obtusoangulatum* Diener
Prionolobus sp. indet. II
Koninckites sp. indet.

Collection 96
Prionolobus cf. *lingtiense* v. Krafft

Collection 107
Gyronites frequens Waagen
Prionolobus sp. indet. I
Flemingites sp. indet. I
Flemingites sp. indet. II
Koninckites sp. indet.
Koninckites cf. *kraffti* Spath
Proptychites sp. indet.
Anakashmirites sp. indet.
"Ophiceras" cf. *obtusoangulatum* Diener

The genera and species of these three collections are characteristic forms of the Lower Ceratite limestone and the Ceratite marls of the Salt Range and the so-called *"Meekoceras"* beds of Spiti, Painkhanda, and Byans of the Himalayas. That is, these faunas are younger than those of the lowest Scythian *Otoceras-Ophiceras* Zone and older than those of the *Owenites* Zone. Spath (1934: 27) recognized a number of zones within two divisions (Gyronitan and Flemingitan) for this part of the geologic column. I am in the process of revising the ammonoids of these horizons from the Salt Range and the Himalayas. It is premature to have a new zonal nomenclature, but extensive changes are indicated. For the purpose of the present discussion the most important thing about these three faunas is that they are not of the lowest Scythian *Otoceras-Ophiceras* Zone. These fossiliferous beds are separated by approximately one meter of unfossiliferous limestone from a horizon that has yielded a varied Permian fauna. The brachiopods of this Permian fauna have been described by Waterhouse (1966),

who concluded they were correlative with the Upper Permian *Cyclolobus* Zone. The corals from these Permian faunas have been reported on by Flügel (1964, 1966). The latest summary of the Permo-Triassic formations of the Salt Range (Kummel and Teichert, 1970, eds.) concludes that most probably one or possibly two stages are missing at the top of the Permian sequence in that area. It would appear that the Permian of Nepal likewise does not include the youngest beds of this system. The one meter bed of unfossiliferous limestone that separates the Permian faunas from collections 95, 96, and 107 may include the *Otoceras-Ophiceras* Zone of lowest Scythian age, but this remains an uncertainty until fossils are found.

I am particularly grateful to Dr. Fuchs for giving me the opportunity to describe these specimens. Dr. R. Sieber of the Geologische Bundesanstalt was also most helpful in the arrangements of this loan.

SYSTEMATIC PALEONTOLOGY

Class CEPHALOPODA Cuvier, 1797

Subclass AMMONOIDEA Zittel, 1884

Family Gyronitidae Waagen, 1895

Genus *Gyronites* Waagen, 1895

Type species, *Gyronites frequens* Waagen, 1895

Gyronites sp. indet.

Plate 3, figures 9, 10

A small, elliptical specimen of approximately 26 mm in diameter and with an umbilical diameter of 8 mm. The conch is compressed, with gently arched lateral areas. The venter is broad and flat.

This genus is the predominant member of the fauna of the Lower Ceratite limestone in the Salt Range of West Pakistan. The specimen recorded here differs from the typical Salt Range species in being slightly more compressed. This difference, however, may be merely a reflection of the preservation. The generic assignment, however, does appear to be correct.

Occurrence. — Collection 107

Repository. — Geologische Bundesanstalt, Vienna.

Genus *Prionolobus* Waagen, 1895
Type species, *Prionolobus atavus* Waagen, 1895; lectotype chosen by Spath, 1934, p. 96

Prionolobus cf. *lingtiense* v. Krafft

Plate 2, figure 4

Meekoceras lingtiense v. Krafft, *in* v. Krafft and Diener, 1909, p. 25, pl. 2, fig. 1; Diener, 1915, p. 193.
Prionolobus lingtiense, — Spath, 1934, p. 102.

A single, distorted, elliptical specimen of approximately 38 mm in diameter; the umbilicus measures about 9 mm in diameter. The lateral areas are broadly convex, ending at an angular ventral shoulder. The venter is broad and arched. No suture is visible. Among the many species from the Lower Triassic of the Salt Range and the Himalayas, this specimen is most similar to *P. lingtiense* v. Krafft. This similarity is most pronounced in the broad, arched venter, and it is on this character that it differs from the specimens described here as *Prionolobus* sp. indet. I and II.

Occurrence. — Collection 96

Repository. — Geologische Bundesanstalt, Vienna.

Prionolobus sp. indet. I

Plate 2, figure 1

A single specimen of approximately 41 mm in diameter and an umbilical diameter of 13 mm. The lateral areas are very gently arched and the venter is narrow and flat. The suture is vaguely visible, showing two lateral lobes and a short auxiliary series. The poor preservation does not allow a specific determination, but assignment to this genus appears fairly secure.

Occurrence. — Collection 107

Repository. — Geologische Bundesanstalt, Vienna.

Prionolobus sp. indet. II

Plate 1, figure 4

A highly distorted, elliptical specimen whose most distinctive feature is a narrow flat venter. This specimen is clearly not conspecific with that recorded here (Pl. 1, fig. 1) as *Prionolobus* sp.

indet. I. The primary difference is the greater umbilical diameter of this species and the greater convexity of the lateral areas. The extreme elliptical distortion of the specimen precludes specific identification.

Occurrence. — Collection 95

Repository. — Geologische Bundesanstalt, Vienna.

Family Flemingitidae Hyatt, 1900
Genus *Flemingites* Waagen, 1892
Type species, *Ceratites flemingianus* de Koninck, 1863

Flemingites sp. indet. I

Plate 2, figure 2

A distorted, elliptical specimen of approximately 70 mm in diameter. The umbilicus measures about 31 mm in diameter, the adoral whorls 25 mm in height and 15 mm in width. The lateral areas are broadly convex and converge on a narrowly rounded venter. No shell or surface markings are preserved. The suture is incompletely preserved but does not show two lateral lobes and a short auxiliary series.

The poor preservation of this specimen does not allow specific comparison. Among the variety of forms assigned to *Flemingites,* this specimen bears most resemblance to *Flemingites glaber* (Waagen, 1895: 188, pl. 11, figs. 2a-d).

Occurrence. — Collection 107

Repository. — Geologische Bundesanstalt, Vienna.

Flemingites sp. indet. II

Collection 107 has a portion of phragmocone that measures about 80 mm in length, with a whorl height of about 40 mm. The sutures are well preserved and typically flemingitid in aspect. The shape of the whorl section and pattern of the suture suggests a strong similarity to *Flemingites compressus* Waagen (1895: 202, pl. 15, fig. 1; pl. 16, fig. 1). The Nepal specimen, however, shows no ribbing of any kind, but this may be the result of preservation.

Occurrence. — Collection 107

Repository. — Geologische Bundesanstalt Vienna.

Family Paranoritidae Spath, 1930
Genus *Koninckites* Waagen, 1895
Type species, *Koninckites vetustus* Waagen, 1895

Koninckites sp. indet.

Plate 1, figures 2, 5

This genus is represented by two poorly preserved, distorted, elliptical specimens. The first (Pl. 1, fig. 2) is approximately 68 mm in diameter and the second (Pl. 1, fig. 5) about 73 mm. The umbilici have diameters of about 8 mm and 9 mm respectively. The flanks are gently arched and the venter narrowly rounded. The suture, though somewhat weathered, clearly shows the two prominent lateral lobes and the developed auxiliary series. The pattern of the suture is similar to that of species of this genus.

The genus *Koninckites* is especially well known from Lower Scythian strata of the Salt Range and the Himalayas. In the Salt Range the genus is a conspicuous member of the fauna from the Lower Ceratite limestone of Waagen (1895), which is the basal part of the Mittiwali Member of the Mianwali Formation of Kummel (1966). In the Himalayas species of this genus occur in the so-called *"Meekoceras"* beds.

Occurrence. — Collection 107

Repository. — Geologische Bundesanstalt, Vienna.

Koninckites cf. *kraffti* Spath

Plate 1, figure 3

Meekoceras varaha Diener, *in*, Krafft and Diener, 1909, p. 17, pl. 2, figs. 4a-d, 2, 3, 5, 6v.; pl. 14, figs. 7, 8; Diener, 1915, p. 195.
Koninckites kraffti Spath, 1930, p. 28; Spath, 1934, p. 155, fig. 43c.

One of the better preserved and least distorted of the specimens can be allied to *Koninckites kraffti*. The specimen has a diameter of approximately 43 mm and is all phragmocone. The umbilicus is small, lateral areas arched, and venter rounded. The suture, though weathered, has two lateral lobes and a well-developed auxiliary series.

Occurrence. — Collection 107

Repository. — Geologische Bundesanstalt, Vienna.

Family Proptychitidae Waagen, 1895
Genus *Proptychites* Waagen, 1892
Type species, *Ceratites lawrencianus* de Koninck, 1863

Proptychites sp. indet.

Plate 1, figure 1

This identification is the least satisfactory of this small assemblage of fossils. The specimen, like most of those in the collection, is distorted and elliptical and no suture is preserved. The assignment to the genus *Proptychites* is suggested by the rounded venter and steep umbilical walls. The whorl section is not very inflated, but this I attribute to a slight crushing of the specimen. The above characters fit well with those of a young specimen of *Proptychites* but not with those of any other genus of this approximate horizon.

Occurrence. — Collection 107

Repository. — Geologische Bundesanstalt, Vienna.

Family Kashmiritidae Spath, 1934
Genus *Anakashmirites* Spath, 1930
Type species, *Danubites nivalis* Diener, 1897

Anakashmirites sp. indet.

Plate 2, figure 7

A distorted, elliptical, highly weathered specimen. It is an evolute form with a whorl whose height is only slightly more than the width. The venter is broad and rounded. Along a small part of the whorl two prominent radial ribs are preserved. The generic assignment of this form appears fairly secure, but the extremely poor preservation does not allow any chance of specific comparisons.

Occurrence. — Collection 107

Repository. — Geologische Bundesanstalt, Vienna.

Family Prionitidae Hyatt, 1900
Genus *Hemiprionites* Spath, 1929
Type species, *Goniodiscus typus* Waagen, 1895.

Hemiprionites typus (Waagen)

Plate 3, figures 6-8

Gonoidiscus typus Waagen, 1895, p. 128, pl. 9, figs. 7, 8a, b, 9, c, 10; Diener, 1915, p. 135; Mathews, 1929, p. 31, pl. 5, figs. 12-21.

Lecanites tahoensis Yehara, 1926, p. 40, pl. 13, figs. 6, 7.
Meekoceras (Gyronites) sawatanum Yehara, 1926, p. 39, pl. 13, figs. 3-5.
Ophiceras tahoensis, — Yehara, 1928, p. 161, pl, 15, figs. 4, 4a, 4b, 5, 7.
Meekoceras sawatanum, — Yehara, 1928, p. 159, pl. 13, figs. 6, 7, 7a, 8, 8a, 9.
Meekoceras katoi Yehara, 1928, p. 157, pl. 15, figs. 3, 3a.
Meekoceras morianum Yehara, 1928, p. 155, pl. 15, figs. 2, 2a, 3, 4, 5.
Meekoceras kuharanum Yehara, 1928, p. 155, pl. 14, figs. 5, 5a.
Goniodiscus americanus Mathews, 1929, p. 32, pl. 5, figs. 22-27.
Goniodiscus walcotti Mathews, 1929, p. 32, pl. 6, figs. 1-5.
Goniodiscus utahensis Mathews, 1929, p. 33, pl. 6, figs. 29-31.
Goniodiscus shumardi Mathews, 1929, p. 33, pl. 6, figs. 11-14.
Goniodiscus slocomi Mathews, 1929, p. 34, pl. 6, figs. 15-17.
Goniodiscus ornatus Mathews, 1929, p. 34, pl. 6, figs. 6-10.
Goniodiscus butleri Mathews, 1929, p. 35, pl. 6, figs. 18-21.
Hemiprionites typus, — Spath, 1929, p. 270; Spath, 1934, p. 330, fig. 114.
Anasibirites (Goniodiscus) ornatus, — Smith, 1932, p. 75, pl. 80, figs. 11,12.
Anasibirites (Goniodiscus) smithi, — Smith, 1932, p. 76, pl. 80, figs. 13-15
Anasibirites (Goniodiscus) typus, — Smith, 1932, p. 76, pl. 31, figs. 11, 12.
Anasibirites (Goniodiscus) utahensis, — Smith, 1932, p. 77, pl. 80, figs. 9, 10.
Meekoceras shikokuense Shimizu and Jimbo, 1933, p. 15.
Hemiprionites americanus, — Spath, 1934, p. 333.
Hemiprionites walcotti, — Spath, 1934, p. 334.
Hemiprionites utahensis, — Spath, 1934, p. 334.
Hemiprionites ornatus, — Spath, 1934, p. 335.
Hemiprionites katoi, — Bando, 1964a, p. 87, pl. 1, figs. 4, 9a-b, 12a-c; Bando, 1964b, p. 7; Bando, 1966, p. 8.
Hemiprionites tahoensis, — Bando, 1964a, p. 88, pl. 1, figs. 7a-b, 8, pl. 2, figs. 4a-b, 18; Bando, 1964b, p. 7; Bando, 1966, p. 8.
Hemiprionites morianus, — Bando, 1964a, p. 89, pl. 2, figs. 1a-c, 2, 9a-b; Bando, 1964b, p. 7; Bando, 1966, p. 8.
Hemiprionites kuharanus, — Bando, 1964a, p. 90, pl. 2, figs. 12a-b; Bando, 1964b, p. 7; Bando, 1966, p. 8.
Hemiprionites kuharanus iyonus Bando, 1964a, p. 91, pl. 1, figs. 14, 18, pl. 2, figs. 15a-b; Bando, 1964b, p. 7; Bando, 1966, p. 8.
Hemiprionites sawatanus, — Bando, 1964a, p. 92, pl. 1, figs. 5a, b, pl. 2, figs. 8a-b, 13a-b; Bando, 1964b, p. 7; Bando, 1966, p. 8.
Hemiprionites shikokuensis, — Bando, 1964a, p. 93, pl. 1, figs. 13, 20, 22, pl. 2, figs. 10a-c; Bando 1964b, p. 7; Bando, 1966, p. 8.
Hemiprionites shimizui Bando, 1964c, p. 335, pl. 49, figs. 1, 2.
Hemiprionites sp. Bando, 1964c, p. 336, pl. 49, fig. 4.

This species is represented by three small, generally poorly preserved specimens. The conch, however, is very distinctive. It is compressed, involute, with a flattened venter and angular ventral

shoulders. This species was first described by Waagen (1895) on specimens from the Upper Ceratite limestone (= upper part of Mittiwali Member of Mianwali Formation, Kummel, 1966) at Chhidru, Salt Range, West Pakistan. The four specimens available to Waagen (1895) are very poorly preserved. The lectotype (Waagen, 1895, pl. 9, figs. 8a, b, c) is a phragmocone of approximately 29.0 mm in diameter with only one side of the conch and the venter preserved. Because of the poor preservation, the serrations on the ventral shoulders and the ribs crossing the venter, as indicated in Waagen's illustration, are doubtful. Only part of the suture is visible and this is highly weathered. One of the paralectotypes (Waagen, 1895, pl. 9, fig. 7) is an extremely poorly preserved specimen in which the only clear feature preserved is the flattened venter. The other paralectotype (Waagen, 1895, pl. 9, fig. 10) is incorrectly represented. The ornament shown in Waagen's illustrations is nothing more than faint growth lines; likewise the specimen bears no serrations on the ventral shoulders.

I have available approximately thirty topotype specimens of this species. Though the preservation leaves much to be desired it is clear that there is much variation in the width of the whorls, width of the flat venter, and umbilical diameter. The Nepal specimens recorded here are directly comparable to a number of the specimens in my Salt Range collection.

Hemiprionites is almost always found in association with *Anasibirites*. The latter genus is a ribbed form which shows fantastic intraspecific variation (Kummel and Erben, 1968). A large number of species has been established for the genus *Anasibirites*. Detailed examination of large collections from Afghanistan and Timor clearly demonstrates the wide range of intraspecific variation. The collection of topotype specimens from Chhidru, Salt Range, West Pakistan, clearly shows that *Hemiprionites typus* is also a species displaying a significant degree of variation in conch parameters. A large number of species has been established on the basis of small and fragmentary specimens from Japan by Yehara (1926, 1928), Shimizu and Jimbo (1933), and Bando (1964a). All these species fall well within the range of variation found in *Hemiprionites typus* from the Salt Range. I can find no basis for separating them from the Salt Range species. The new species, *Hemiprionites dunajensis* Zakharov (1968) from the Primorye Region, appears likewise to be nearly identical with *H. typus*. I can find no basis for separating this form from the type species. The *Anasibirites* fauna of Fort Douglas, Utah, has yielded a well-preserved fauna including *Hemiprionites*. Mathews (1929), who

made the original study, and Smith (1932), who was first revisor, established a large number of new species of *Hemiprionites,* at the same time assigning some of their specimens to the type species. Here again analysis of topotype material shows that all these species are based on characteristics that are highly variable. The fossil beds from which these specimens are derived strongly suggest a unified, interbreeding population. I find no criteria within these forms to separate them from *Hemiprionites typus.*

Though *Hemiprionites* is geographically fairly widespread there are relatively few species. Within Tethys, in addition to *Hemiprionites typus,* there is *H. hungeri* Kummel (in Kummel and Erben, 1968) from the *Anasibirites* Subzone at Kotal-e-Tera, Afghanistan. This species is distinctive in the evolute nature of the conch and the closely spaced transverse, thin ribs on the venter. I find the Timor *Hemiprionites timorensis* somewhat of an enigma. On the one hand, the general conch morphology of this species is very similar to that of *H. typus,* on the other, Spath (1934: 332) writes of transitional forms to *Anasibirites multiformis.* Hopefully a larger sample of specimens of this species will become available. The Spitsbergen *Hemiprionites garwoodi* Spath (1934: 336) is another distinctive species in its irregular lateral ribs.

Occurrence. — Collection 110

Repository. — Geologische Bundesanstalt, Vienna.

Family Sibiritidae Mojsisovics, 1896
Genus *Anasibirites* Mojsisovics, 1896
Type species, *Sibirites kingianus* Waagen, 1895

Anasibirites kingianus (Waagen)

Plate 3, figures 1-5

Sibirites kingianus Waagen, 1895, p. 108, pl. 8, figs. 1a-c, 2a-c.
Anasibirites sp. Bando, 1964c, p. 337, pl. 49, figs. 3a-c.
Anasibirites kingianus, — Kummel and Erben, 1968, p. 135, pl. 20, figs. 6, 7, pl. 22, figs. 12-17, pl. 23, figs. 1-18.
Anasibirites multiformis Nakazawa and Bando, 1968, p. 96, pl. 5, figs. 2-5.
Anasibirites nevolini Zakharov, 1968, p. 131, pl. 25, figs. 4-5.

This genus and species was extensively reviewed by Kummel and Erben (1968) in their discussion of a rich mid-Scythian fauna from Kotal-e-Tera, Afghanistan. The genus is widely distributed and in many places has yielded an abundance of well-preserved

specimens. The characteristic ornamentation of the genus has given the typologist a field day in the establishment of new species. Analysis of the large collection from Kotal-e-Tera, Afghanistan, has shown that the pattern of ornamentation is highly variable and gradational in nearly every respect. The conclusion was that there is only one species of *Anasibirites*. The specimens recorded here from Nepal are typical forms, differing in no way from previously described and illustrated specimens considered to be *Anasibirites kingianus*. This genus and species is now known from a number of localities in Tethys and the circum-Pacific region. It is well represented at Kotal-e-Tera, Afghanistan, as mentioned above; in the Upper Ceratite limestone of the Salt Range, West Pakistan; in the Himalayas of northern India; in South China; Timor; western Australia; Japan; the Primorye Region; and in western United States.

Occurrence. — Collection 106 (Pl. 3, fig. 1), collection 110 (Pl. 3, figs. 2-5).

Repository. — Geologische Bundesanstalt, Vienna.

Genus Uncertain
"Ophiceras"? cf. *obtusoangulatum* Diener

Plate 2, figures 3, 5, 6

Ophiceras obtusoangulatum Diener, *in* v. Krafft and Diener, 1909, p. 82, pl. 37, fig. 6.

There are two specimens in the collection that are very similar to Diener's species from the *"Meekoceras"* beds at Lilang in the Himalayas. The species was established on the basis of a single specimen. I cannot accept Diener's assignment of his species to the genus *Ophiceras*, primarily on the tabulate nature of the venter. At the same time there are no other Lower Scythian genera to which this form can be assigned. It is most probable that this form represents a new genus, but on the basis of the material available it would be unwise to establish a new genus at this time.

The Nepal specimens are both distorted and elliptical with the inner whorls especially poorly preserved. The conches are widely evolute, the whorls compressed, converging toward a narrow, subtabulate venter bordered by subangular shoulders. The suture consists of a large first lateral lobe, a smaller second lateral lobe, and a short auxiliary series on the umbilical shoulder and wall.

Occurrence. — Collection 95 (Pl. 2, fig. 3), collection 107 (Pl. 2, figs. 5, 6).

Repository. — Geologische Bundesanstalt, Vienna.

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(Received 4 December 1969.)

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EXPLANATION OF PLATE 1

Fig. 1. *Proptychites* sp. indet. I, from collection 107, × 1

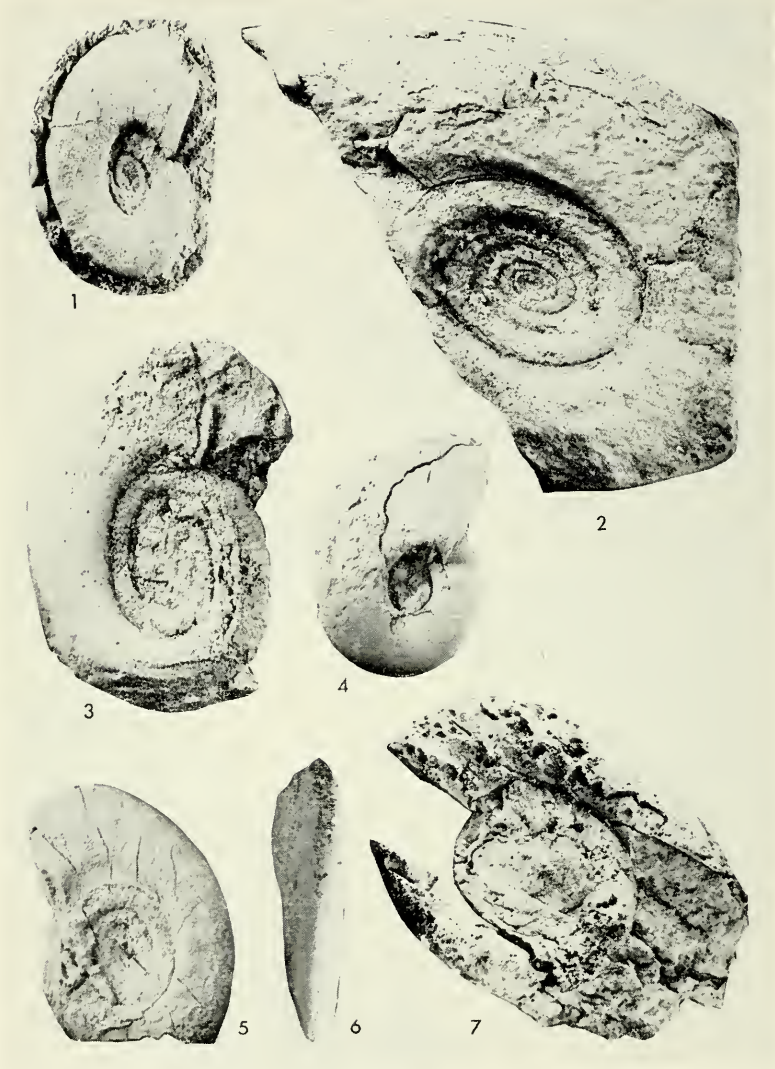
Fig. 2. *Koninckites* sp. indet., from collection 107, × 1

Fig. 3. *Koninckites* cf. *kraffti* Spath, from collection 107, × 1

Fig. 4. *Prionolobus* sp. indet. II, from collection 95, × 1

Fig. 5. *Koninckites* sp. indet., from collection 95, × 1

All specimens are from Lower Triassic of Nepal and are deposited in the Geologische Bundesanstalt, Vienna.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EXPLANATION OF PLATE 2

Fig. 1. *Prionolobus* sp. indet. 1, from collection 107, × 1

Fig. 2. *Flemingites* sp. indet. 1, from collection 107, × 1

Fig. 3. *"Ophiceras"* cf. *obtusoangulatum* Diener, *in* v. Krafft and Diener (1909) from collection 95, × 1

Fig. 4. *Prionolobus* cf. *lingtiense* v. Krafft, *in* v. Krafft and Diener (1909) from collection 96, × 1

Fig. 5, 6. *"Ophiceras"* cf. *obtusoangulatum* Diener, *in* v. Krafft and Diener (1909) from collection 107, × 1

Fig. 7. *Anakashmirites* sp. indet., from collection 107, × 1

All specimens are from Lower Triassic of Nepal and are deposited in the Geologische Bundesanstalt, Vienna.

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EXPLANATION OF PLATE 3

Figs. 1-5. *Anasibirites kingianus* (Waagen). Fig. 1 from collection 106, ×1. Figs. 2-5 from collection 110, Fig. 2, × 2, Figs. 3-5, × 1

Figs. 6-8. *Hemiprionites* sp. indet., from collection 110, × 1.5

Figs. 9-10. *Gyronites typus*, from collection 107, × 1.5

All specimens are from Lower Triassic of Nepal and are deposited in the Geologische Bundesanstalt, Vienna.

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CAMBRIDGE, MASS. 3 APRIL, 1970 NUMBER 346

NEW FROGS OF THE GENUS *BATRACHYLODES* (RANIDAE) FROM THE SOLOMON ISLANDS

Walter C. Brown[1] and Fred Parker[2]

ABSTRACT. Prior to 1963, only two lowland species of the genus *Batrachylodes* (Ranidae) were recognized from the Solomons archipelago. In the past few years intensive sampling of the populations of frogs in the mountain areas of Bougainville has revealed the presence of eight species of this endemic genus. Brief note is also made of their known geographic distribution in the archipelago as well as their zonal distribution in the mountains.

INTRODUCTION

In this paper, the second based on the extensive collections of amphibians obtained by the junior author on Bougainville Island, Solomon Islands, new species of the endemic ranid genus *Batrachylodes* are described.

The genus was set up by Boulenger (1887, p. 337) to accommodate a single species, *vertebralis*. Sternfeld (1921, p. 435) described two frogs from Buka Island which he regarded as microhylids. He named these *Sphenophryne wolfi* and *Chaparina frederici,* each based upon a single specimen. Mertens (1929, p. 266) sank both in the synonomy of *Batrachylodes vertebralis*. Brown and Myers (1949, p. 379) described *B. trossulus* from Bougainville Island.

The collections made by the junior author on Bougainville Island during the period 1961-63 and 1966 contain samples of eight species. Re-examination of the types of *Chaperina frederici* and *Sphenophryne wolfi* confirms the fact that the former is synonymous with *B. vertebralis* (northern Bougainville population). However, our present large series indicates that *B. wolfi* is distinct from

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B. vertebralis. Thus, three species of this genus have been previously recognized and described. The other five species are new.

All collections previously assigned to *B. vertebralis* from various islands in the Solomons Archipelago should now be re-examined in terms of our present knowledge. Some of these specimens, usually representing very small samples, may actually belong to some other of the large-disked species.

Measurements, determined to the nearest 0.1 mm, with a Helios dial caliper, are based on preserved specimens. Snout-vent length is the distance from the tip of the snout to the vent with the specimen held flat, ventral surface down; the tibia length is the length of the bone of the lower leg; the head length is the distance from the tip of the snout to the posterior edge of the tympanum; head breadth is measured at the angle of the jaws; diameter of the eye is from the anterior to the posterior edge of the socket; first and fourth finger lengths from the tip to the base of the subarticular tubercle; third and second finger lengths from the tip to the base of the second articular tubercle; interorbital distance is breadth of the bone between the eyes. Methods of determining other measurements such as breadth of disks are probably not subject to much variation.

Specimens in the collections of various institutions are identified as follows: Museum of Comparative Zoology, Harvard University (MCZ); Division of Systematic Zoology, Stanford University (SU); British Museum of Natural History (BMNH); Senckenberg Museum, Frankfurt am Main (SMF); and, California Academy of Sciences (CAS).

DESCRIPTIONS OF SPECIES

The genus can, arbitrarily, be conveniently divided into two groups of species: (1) Those with broadly dilated finger disks (except for the inner finger), the breadth of the disk of the third finger is very rarely less than 35 per cent the length of the third finger as measured to the base of the second subarticular tubercle, much more broadly dilated than the largest toe disk; (2) Those species in which the tips of the fingers are not or but moderately dilated, the breadth of the disk of the third finger very rarely more than one-third the length of the third finger, less than to about equal to the breadth of the largest toe disk. The first group, with the exception of *B. vertebralis,* are all relatively large species; the second group are small species.

Small-disked species

Batrachylodes trossulus Brown and Myers

Batrachylodes trossulus Brown and Myers, 1949, Journ. Washington Acad. Sci., 39: 379-80; Torokina, Bougainville I. (type in United States National Museum).

Definition. A small *Batrachylodes,* snout-vent length for 19 mature males ranging from 18.1 to 20.8 mm (Table 1), and for 20 mature females from 18.1 to 22.7 mm (a female 17.3 mm in snout-vent length is immature); tips of fingers scarcely to slightly dilated, ventral part delimited by a circummarginal groove; first finger shorter than second which is slightly shorter than to equal to fourth (Fig. 1); breadth of disk of third finger about 15 to 25 per cent of length of third finger; disks of toes larger than those of fingers, toes with minute webs at base; hindlimbs relatively long, length of tibia about 48 to 55 per cent of snout-vent length; breadth of head about 62 to 73 per cent of length of tibia (Table 2). More than 100 specimens were examined, including MCZ 74824-79.

Color. A blackish band with a smooth dorsal margin extending from the tip of the snout through the eye and ear to the groin or nearly to the groin, becoming narrower on the posterior part of the trunk, under surface of head, throat and usually pectoral region dusky to brown or blackish; dorsum grayish cream to reddish or brownish gray, more or less uniform, or with darker markings, most frequently a small to moderate, dark chevron in the region of the forelimbs.

Distribution. Known from both northern and southern collecting sites of Bougainville Island, as well as the type locality, Torokina, on the central west coast, and possibly Choiseul Island (see Brown and Myers, 1949). It is recorded at elevations from near sea level to about 4000 feet.

Batrachylodes minutus sp. nov.

Holotype. MCZ 41391, an adult female, collected by Fred Parker in the Aresi area, at 2000 feet elevation, on Bougainville Island, Solomon Islands, 14 April 1963.

Paratypes. (all collected by Fred Parker on Bougainville Island) MCZ 41390, from the Aresi area, at 2000 feet elevation, 14 April 1963; MCZ 55534, from Melilup, between 2500 and 3500 feet elevation, collected 14 May 1966; MCZ 55037-49, 55521-28, 55533-40, 55546, 62020-23, SU 23989, 23991-92, from Mutahi, between 2200 and 3500 feet elevation, collected between 9 and

20 May 1966. MCZ 36924 (9 September 1962), MCZ 41386 (25 December 1962), and SU 21852 (30 December 1962), from Pipekei area, between 1000 and 2000 feet elevation.

Diagnosis. A small *Batrachylodes,* measuring about 16 to 19.5 mm in snout-vent length for 20 mature specimens available; disks of fingers not or scarcely dilated (Fig. 2, left), ventral part rather vaguely delimited by a shallow circummarginal groove; first finger usually shorter than but occasionally nearly equal to second, which is equal to or slightly longer than fourth when adpressed; disks of toes larger than those of fingers; toes with minute webs at base; tibia usually less than 48 per cent of snout-vent length; breadth of head about 70 to 78 per cent of length of tibia; without broad, blackish band on lateral surfaces, under surface of head and throat more or less dusky to brown or blackish.

Description. Snout-vent length of 16 mature females 16.7 to 19.3 mm (a female measuring 16.3 is apparently immature judging by the fact that the oviducts are straight and undilated), of seven mature males 15.8 to 17.7 mm (Table 1); hindlimbs moderate, length of tibia ranging from about 43 to 53 per cent of snout-vent length; breadth of head slightly less to slightly greater than length of head, and from 70 to 85 per cent of length of tibia (Table 2); eye moderately large, its diameter slightly less to slightly greater than length of snout, and about 31 to 48 per cent of breadth of head; tympanum distinct, about 50 per cent of diameter of eye; canthus rostralis broadly rounded; loreal region nearly vertical; tongue without notch posteriorly; a fold dorsal and posterior to tympanum; fingers slender, without webs, tips scarcely expanded (Fig. 2); ventral pad rather vaguely delimited by a circummarginal groove, breadth of disk of third finger about 14 to 24 per cent of length of third finger (Table 2); first finger usually shorter than second which is longer than or about equal to fourth when adpressed; hindlimbs moderately long; subarticular tubercles large, elliptical, scarcely protruding; inner and outer metacarpal tubercles relatively large and flattened; length of tibia about 43 to 52 per cent of snout-vent length; toes webbed at base; tips of toes moderately dilated; breadth of disk of third toe about 1.38 to 2.33 times breadth of the disk of third finger; subarticular tubercles large, broadly oval, and not strongly protruding; inner metatarsal tubercle large, broad, reaching nearly to subarticular tubercle of first toe; outer metatarsal tubercle low and round, or scarcely evident.

Color (in preservative). Dorsum variable, ground color light greenish olive, greyish olive, or brownish; sometimes with variable

dark or blackish blotches and flecks, forming an irregular interorbital patch and a crude, hourglass pattern, more or less complete, on the dorsum between the forelimbs and the groin; a narrow to moderate, often much interrupted, blackish band from the snout to the region of the tympanum or the forelimbs usually evident; anterior edge of thighs, posterior edge of metatarsal area, and sole of foot also usually marked with a dusky to blackish, irregularly margined band; upper surface of hindlimbs with three more-or-less distinct, broad, dark, transverse bands, blackish, irregular crescent at the anal region; a dusky patch on the posterior surface of the distal part of the thigh and proximal tibia. Under surface of head, throat, and pectoral region heavily marked with dark flecks; abdominal region lighter.

Measurements of type. Snout-vent length 17.6 mm; length of head (to posterior edge of tympanum) 6.2 mm; breadth of head 5.9 mm; diameter of eye 2.5 mm; diameter of tympanum 1.2 mm; length of snout 2.2 mm; length of tibia 8.4 mm; length of third finger to base of proximal subarticular tubercle 2.1 mm; breadth of disk of third finger 0.4 mm; breadth of disk of third toe 0.8 mm.

Distribution. Known from collecting sites on both southern and northern Bougainville Island at altitudes from about 1000 to 3000 feet.

Juveniles. MCZ 41387, a juvenile measuring 8 mm in snout-vent length, is not included in the paratypic series, but is tentatively assigned to this species. In general color pattern, it is less distinct from *B. trossulus* than are the adults with which it was taken.

Comparisons. B. minutus, in size and relative lack of dilation of the finger disks, is most similar to *B. trossulus.* It differs in its smaller size at maturity (Table 1); the slightly broader head relative to the snout-vent length, the greater length of the tibia relative to the breadth of the head, the shorter third finger relative to the breadth of the head (Table 2); and noted features of the color pattern, especially the greatly reduced and less conspicuous dark brown to blackish bands on the sides of the head and body.

Batrachylodes mediodiscus sp. nov.

Holotype. MCZ 41589, an adult male, collected by Fred Parker in the Pipekei area, at 2000 feet elevation, on Bougainville Island, Solomon Islands, 29 December 1962.

Paratypes. (all collected by Fred Parker on Bougainville Island) MCZ 44056 (5 August 1963), 41682-83 (13 April 1963), and SU 21812 (1 May 1963), Aresi area, between 600 and 1500

feet; MCZ 38066, 41650, and BMNH 1964-690 (22 January 1963), 38255 (26 February 1963), MCZ 41600-01 (31 December 1962), MCZ 41692-93 (16 April 1963), 41694-95 (1 May 1963), 42295, MCZ 42438 (28 June 1963), MCZ 44148 (28 July 1963), 44162-63 (7 August 1963), 44174-75 (15 September 1963), Kunua area, foothills, between 100 and 1000 feet elevation; MCZ 74101-04, Lake Loloru, between 4000 and 4300 feet elevation, collected 31 March 1963; MCZ 53111, 53124, 53127-29, 53131-34, 53136-38, 53141-45, 53151-53, 53156-57, 53159-66, 53168-74, 53178-94, 53196, 53198-205, 53208-27, 53229-45, 53247-59, 54777-82, 55016-79, 55523-25, 55541-42, 55547, 71082-453, 73272-77, 74105, 74470-722, 74732-823, 76679-80, 79653, Mutahi, between 1800 and 3900 feet elevation, collected between 9 and 20 May 1966; MCZ 55005-6, Pamauita, at 1200 feet elevation, collected 23 March 1966; MCZ 41584-88, 41593, 41599, SU 21814, and SMF 60016, Pipekei, between 2000 and 3200 feet elevation, collected between 29 and 31 December 1962; SU 21815, Pipekei, foothills, 500 feet elevation, collected December 1962; MCZ 55552-53, Topanas, collected 8 May 1966.

Diagnosis. A *Batrachylodes* of moderate size, snout-vent length of mature specimens ranging from about 21 to 25 mm in our present sample (Table 1); disks of fingers and toes usually about equally dilated; breadth of disk of third toe about 90 to 125 per cent of breadth of disk of third finger; breadth of disk of third finger 23 to 34 per cent of length of third finger, and about 35 to 60 per cent of diameter of tympanum.

Description. Snout-vent length of 20 mature females 21.7 to 27.0 mm (a female measuring 20 mm in snout-vent length is immature), of 22 mature males 21.6 to 25.8 mm (Table 1); hindlimbs relatively long, length of tibia ranging from 48 to 57 per cent of snout-vent length for 20 specimens; breadth of head slightly less than to slightly greater than its length and about 66 to 79 per cent of length of tibia; length of snout greater than diameter of eye; eye moderate, its diameter 27 to 39 per cent of breadth of head; tympanum distinct, its diameter about 60 to 70 per cent of diameter of eye; canthus rostralis rounded; loreal region only moderately oblique, not markedly concave; tongue with a shallow notch posteriorly or entire; a low to moderate fold dorsal and posterior to tympanum; fingers moderately slender, without webs, tips expanded into moderate disks; breadth of disk of third finger about 23 to 35 per cent of length of third finger, usually slightly less than breadth of disk of third toe (Table 2), and about 35 to 60 per cent

of diameter of tympanum; ventral pad of finger disks separated from dorsal part by a circummarginal groove; first finger shorter than second which is somewhat shorter than to about equal to the fourth when adpressed; subarticular tubercles moderately large but not strongly protruding; outer metacarpal tubercle round; inner broadly oval; median tubercle large (Fig. 2); tips of toes expanded into moderate disks, usually slightly larger than those of fingers, breadth of disk of third toe 90 to 125 per cent of breadth of disk of third finger for 20 specimens (Table 2); ventral part of disk separated from dorsal part by a circummarginal groove; subarticular tubercles moderate, not strongly protruding; inner metatarsal tubercle narrow, elongate; outer small, round.

Skin of dorsum usually with a few short, narrow, raised folds which are associated with the dark pigmented spots; venter relatively smooth except for the small white tubercles of chin and throat of males; posterior thighs granular.

Color (in preservative). Dorsal ground color variable, ranging from greyish tan, through greyish olive to dark brown; a small blackish spot on either side of the middorsal line in the axillar region, often more elaborate, suggesting a "V" or spread "H," least obvious in the more melanistic individuals; usually a dark blotch or spots on the dorsum at the anterior end of the pelvic girdle; a dusky to black line from the snout posterior to the tympanic region or, at times, continued on the flanks; anterior and posterior thighs and anal region with irregular dusky to blackish markings; two dark transverse bands more or less evident on the thighs; venter uniformly light, or variously mottled with brown, especially on under surface of head and throat.

Measurements of type. Snout-vent length 23.6 mm; length of head to posterior edge of tympanum 9.0 mm; breadth of head 9.1 mm; diameter of eye 3.0 mm; diameter of tympanum 2.1 mm; length of snout 3.5 mm; length of hindlimb 37.0 mm; length of tibia 11.7 mm; length of third finger 3.0 mm; diameter of disk of third finger 0.9 mm; diameter of disk of third toe 1.0 mm.

Distribution. In addition to the large type-series from both northern and southern sites of Bougainville Island, eleven specimens MCZ 41238-43, 41671-72, 55007; and SU 21811, 21813 from Buka Island are referred to this species. The known altitudinal range extends from the coastal plains to about 4000 feet.

Comparisons. B. mediodiscus is larger in size at maturity than *B. minutus* or *B. trossulus,* and the disks of the fingers (except the first) are more broadly dilated, being about equal to those of the toes.

Large-disked species

The large-disked species are much less easily distinguished on the basis of conspicuous key-characters than are the small-disked species. In some instances, it is difficult to assign individual specimens, especially juveniles, to a given species, as is in some instances true for other frogs, for example, some species of *Platymantis.* However, such species are frequently distinguishable in the field on the basis of habits, behavior, and/or voice characteristics. Adequate samples may then usually be separated on the basis of a combination of morphological characters. The large-disked species of *Batrachylodes* are such a group. These species include *B. vertebralis* (the type species), *B. wolfi,* and three previously undescribed. These are considered in the following pages.

Batrachylodes wolfi (Sternfeld)

Sphenophryne wolfi Sternfeld, 1921, Abhand. Senckenberg. Naturf. Ges., 36, p. 435: Buka I., Solomon Islands (type in Senckenberg Museum).

Batrachylodes vertebralis (part), Mertens, 1929, Zool. Anz., 80, p. 266.

This is one of the large species of this genus, as measured by snout-vent length at maturity (Table 1). Although individual specimens of this species and *B. vertebralis, B. elegans,* or *B. montanus* might be confused, representative samples are readily distinguished on the basis of a combination of several characteristics, as indicated in the comparisons. *Batrachylodes wolfi* is, therefore, resurrected from the synonomy of *Batrachylodes vertebralis.*

Definition. A large *Batrachylodes,* snout-vent length of 20 mature males 25.2 to 30.6 mm, of 24 mature females 28.2 to 31.7 mm (Table 1) (a female measuring 26.5 mm snout-vent is immature, judging by the straight, undilated oviducts); tips of fingers broadly dilated (Fig. 3), much broader than tips of toes, breadth of disk of third finger about 38 to 55 per cent of length of third finger, breadth of disk of first finger 50 to 67 per cent of breadth of disk of third finger; first finger much shorter than second which is about equal to fourth when adpressed (77 to 88 per cent as measured); length of third finger about 35 to 45 per cent of length of head; disks of toes less broadly dilated than those of finger; toes with very minute webs at base; length of tibia usually less than 45 per cent of snout-vent length; head relatively broad, breadth greater than 80 per cent of length of tibia; interorbital breadth about 116 to 150 per cent of length of third finger, and 73 to 92 per cent of length of fourth finger (Table 3). More than 100 specimens were examined, including MCZ 54135-325.

Color. Dorsum greenish (olive green in life), occasionally dark brown for melanistic specimens, generally uniform or nearly so; a moderate, blackish band (in life), its breadth about one-third to one-half the depth of the loreal, extending from the tip of the snout through the eye and the tympanum and remaining more or less uniformly broad until reaching the post-axillary region where it may disappear or fade gradually toward the groin; dark transverse bars on hindlimbs usually absent; venter creamy white in typical color pattern, brownish in melanistic specimens.

Distribution. Presently recorded from both northern and southern sites on Bougainville (elevation from near sea level to about 4000 feet), and from Buka Island.

Comparisions. Based on the Bougainville samples, *B. wolfi* is slightly larger at maturity, both mean and maximum snout-vent length, for both males and females, than *B. vertebralis,* and smaller than *B. elegans, B. montanus,* and *B. gigas* (Table 1). *B. wolfi* exhibits less variation in color for the large sample (500+ specimens), and more uniform dorsal coloration of individual specimens than other species of this large-disked group, with the exception of some examples of *B. elegans.* The dorsal ground color of *B. wolfi* is also, except for some melanistic examples, more yellowish or olive green than is characteristic of other species.

The disk of the first finger appears more broadly dilated on the average than the first finger disks of other species, with the exception of *B. gigas.* This is also supported in the ratio of the breadth of the first finger disk to the breadth of the third finger disk (Table 3). The mean ratio of the interorbital distance to the length of the fingers is greater than the mean ratio for the other species, with the exception of the population referred to *B. vertebralis* from northern Bougainville.

For *B. wolfi,* the undersurface of the legs is uniformly light, not flecked or blotched with brown, as in *B. elegans,* and the iris is reddish in life, in contrast to the silver-grey iris of *B. elegans. B. wolfi* may be further distinguished from *B. gigas* by the breadth of the finger disks relative to length of fingers, for example, the breadth of the third finger disk to the length of the third finger (Table 3); and from *B. montanus* by the much shorter third finger relative to the length of the head (Table 3).

Batrachylodes vertebralis Boulenger

Batrachylodes vertebralis Boulenger, 1887, Proc. Zool. Soc. London, 1887, p. 337, pl. xxviii, fig. 3; Fauro I., Solomon I. (type in British Museum).

Chaperina frederici Sternfeld, 1921, Abhand. Senckenberg. Naturf. Ges., 36, p. 435; Buka I., Solomon Islands (type in Senckenberg Museum).

Fauro Island, the locality for the unique specimen upon which *B. vertebralis* was based, is located at the southern end of Bougainville Island, from which it is separated by a distance of 9 km or slightly less. A small island lying in the passage divides it into two channels and further reduces the actual overwater distance by nearly half. A sample from the population of this species occurring on southern Bougainville Island is in reasonable agreement with the type, including size at maturity. On the contrary, no individual of a sample of more than 100 specimens from the northeastern part of Bougainville is as large as the type. Boulenger (1887, p. 337) gives the snout-vent length of the holotype, a mature female, as 30 mm; our measurement, using a vernier caliper (see methods), is 28.1 mm. The largest female in our present sample from southern Bougainville is 29.5 mm.

The following definition of the species is based upon a sample of specimens from the southern end of Bougainville, including MCZ 73800-73871.

Definition. A moderate-sized to large *Batrachylodes,* snout-vent length ranges from 25.4 to 29.5 mm for 5 mature females, and 21.4 to 28.6 mm for 18 males (Table 1) (several females between 23.0 and 24.0 mm in snout-vent length are not yet mature, judging by the straight, undilated oviducts); breadth of head 75 to 97 per cent of length of tibia; interorbital breadth 57 to 61 per cent of length of fourth finger, 47 to 54 per cent of length of third finger; tips of fingers, except for the first, broadly dilated (Fig. 3, right), much broader than tips of toes; breadth of disk of third finger about 33 to 43 per cent of length of third finger and 73 to 94 per cent of length of first finger; disk of first finger scarcely dilated, about 40 to 53 per cent of breadth of disk of third finger; first finger much shorter than second, its length being 70 to 80 per cent the length of the latter (as measured); the second slightly shorter than or equal to fourth when adpressed; disks of toes much less broadly dilated than those of fingers; breadth of disk of third toe 71 to 87 per cent of breadth of disk of second finger; toes with minute webs at base; length of tibia 43 to 52 per cent of snout-vent length; head breadth usually less than 80 per cent of length of tibia (Table 3).

Color. Dorsum grayish cream to tan to brownish, darker markings in various patterns, occasionally with a light vertebral strip; a dark line or narrow band with irregular dorsal margins or a series

of blotches from the tip of the snout through the eye and the dorsal part of the tympanum, with a deep indentation anterior to the forelimbs, dark transverse bands of the hindlimbs; usually brownish mottled, at least anteriorly.

Variation. The sample of the population from northern Bougainville which is referred to *B. vertebralis* differs from the sample of population of southern Bougainville in a number of characteristics: the generally smaller size at maturity for both males and females (Table 1); the greater frequency of lighter shades of color (grayish) in the dorsal ground color; and, the somewhat broader interorbital relative to length of the fingers, length of head, and length of snout (Table 4). The call, as observed in the field, appears identical. The noted differences are sufficiently great that these two populations may well prove to be distinct subspecies. However, since we do not have information regarding the characteristics of samples from the more central areas of Bougainville, we have chosen, for the present, to hold in abeyance a decision as to the taxonomic importance of the observed differences.

Distribution. B. vertebralis is recorded from numerous islands throughout the archipelago (Brown, 1952), but in view of the number of morphologically similar species which are now known, the collections upon which the records are based should be redetermined. The population in southern Bougainville ranges from sea level to about 4000 feet; the population on northern Bougainville ranges from sea level to about 3000 or 3500 feet.

Comparisons. Differences in size relative to the other large-disked species and several characteristics which distinguish *B. vertebralis* from *B. wolfi* have been noted in the previous section. *B. vertebralis* may be further distinguished: from *B. gigas* on the basis of the smaller third toe disk relative to breadth of the disk of second or third fingers; from *B. montanus* by the greater breadth of interorbital relative to the breadth of the disk of third finger and the larger tympanum relative to the third finger disk; and, from *B. elegans* by the usually smaller tympanum relative to the third finger disk (Tables 3 and 4).

Batrachylodes gigas sp. nov.

Holotype. MCZ 73764, an adult female, collected by Fred Parker in the Lake Loloru area, at 4300 feet elevation, on Bougainville Island, Solomon Islands, 31 March 1966.

Paratypes. (all collected by Fred Parker on Bougainville Island) MCZ 62018-19, 73765, and CAS 117442 from Lake Loloru, 4300 feet elevation, collected 31 March 1966.

Diagnosis. A large *Batrachylodes,* snout-vent length of 42.5 to 46 mm for three mature females (Table 1); breadth of disk of first finger usually more than 50 per cent of breadth of disk of third finger; breadth of disk of third finger less than 40 per cent of length of third finger, 65 to 75 per cent of the length of first finger, and 55 to 75 per cent of interorbital breadth; breadth of disk of third toe about 90 to 95 per cent of the breadth of disk of second finger and 65 to 85 of breadth of disk of third finger; diameter of tympanum about 80 to 110 per cent of breadth of disk of third finger; interorbital distance relatively narrow, about 95 to 100 per cent of length of first finger, 30 to 40 per cent of length of third finger and 20 to 22 per cent of length of head; first finger shorter than second, which is much shorter than fourth when adpressed; and, an irregularly margined dark or blackish band or blotches on anterior thigh, inner surface of tibia, and lower surface of tarsus.

Description. Snout-vent length of three mature females 42.7 to 46 mm (two females 34 mm in snout-vent length are immature, as judged by the straight, undilated oviducts); hindlimbs moderately long, length of tibia 44 to 52 per cent of snout-vent length for five specimens; breadth of head slightly less than to slightly greater than its length, and about 80 to 97 per cent of length of tibia; eye moderate, diameter of the eye about 80 to 100 per cent of length of snout; tympanum distinct, its diameter about 46 to 55 per cent of diameter of eye; interorbital distance about 20 to 22 per cent of head length, less than 55 per cent of length of third finger, and usually slightly less than length of first finger (Table 3); canthus rostralis rounded; loreal region moderately oblique, only slightly concave; tongue entire, truncate posteriorly or with a minute notch posteriorly; a fold dorsal and posterior to the tympanum; fingers without webs, the tips broadly dilated except for that of first; breadth of disk of first finger about 50 to 62 per cent of breadth of disk of third finger; breadth of disk of third finger about 31 to 39 per cent of length of third finger; and about 80 to 110 per cent of diameter of tympanum; ventral pad of disks separated from dorsal part by a circummarginal groove; first finger shorter than second, which is shorter than fourth when adpressed; subarticular tubercles moderately large but not strongly protruding; inner metacarpal tubercle small, low, and rounded; middle one broadly oval; outer one elongate (Fig. 1); tips of toes expanded into moderate disks,

smaller than those of fingers, breadth of disk of third toe about 65 to 85 per cent of breadth of disk of third finger, and 90 to 95 per cent of breadth of disk of second finger (Table 3); ventral part of disk separated from dorsal part by a circummarginal groove; subarticular tubercles moderately large, rather low; inner metatarsal tubercle elongate, oval; outer small, round; toes with a very shallow web at the base, except between the first and second.

Skin of dorsum and venter smooth; posterior surface of thighs with low, flattish granules.

Color (in preservative). Dorsum variable, from light grayish olive or light brownish olive to salmon red; a dark interorbital bar and a dark "W" just posterior to the head are usually distinct; lateral surface of head through eye and tympanum and upper lateral surface of anterior part of body marked by a blackish band which tapers and fades posteriorly; lower lateral surfaces and anterior part of venter or entire venter densely marked by dark flecks; posterior surface of lower arm and both anterior and posterior surface of thighs with irregularly margined dark longitudinal bands; moderate, dark, transverse bands on hindlimbs may be strongly or only faintly marked.

Measurements of type. Snout-vent length 46.0 mm; length of head to posterior edge of tympanum 16.6 mm; breadth of head 17.6 mm; diameter of eye 5.5 mm; diameter of tympanum 2.6 mm; length of snout 6.7 mm; interorbital distance 3.75 mm; length of hindlimb 69.4 mm; length of tibia 24.0 mm; length of third finger 7.1 mm; diameter of disk of third finger 2.8 mm; diameter of disk of third toe 1.9 mm; length of first finger 3.75 mm; first finger disk 1.55 mm; length of second finger 4.55 mm; second finger disk 2.2 mm; length of fourth finger 6.3 mm; fourth finger disk 2.55 mm.

Distribution. Known only from the type locality in the mountains near Lake Loloru area at the southern end of Bougainville Island at altitudes of about 4000 to 5000 feet.

Comparisons. This is the largest known member of the genus. The smallest of the three mature females (preserved state) measures 42.7 mm and the largest 46 mm in snout-vent length. Males of this species are unknown. As compared to the other three broad-disked species, the disks of the fingers are slightly less dilated; the breadth of the disk of the third finger is less than 75 per cent of the length of the first finger (usually greater than 80 per cent for the other large-disked species), and less than 40 per cent of the length of the third finger length (usually greater than 40 per cent for the rest of the species other than *vertebralis* from the

southern part of Bougainville). The disk of the third toe is almost as large as the disk of the second finger – 90 to 95 per cent (usually less than 90 per cent for the other large-disked species). The interorbital distance relative to the length of the fingers is usually less than for other large-disked species with the exception of *B. montanus.* The breadth of the disk of the first finger is about 50 to 60 per cent of the breadth of the disk of the third finger. In this ratio *gigas* resembles *wolfi,* whereas the other large-disked species usually show this ratio as less than 50 per cent.

Batrachylodes elegans sp. nov.

Holotype. MCZ 54559, an adult female, collected by Fred Parker at Mutahi, between 2200 and 3200 feet elevation, on Bougainville Island, Solomon Islands, 16 May 1966.

Paratypes. (all collected by Fred Parker on Bougainville Island) MCZ 54333, 54337, 54339, 54341, 54345-47, 54353, 54358, 54361, 54363, 54365-66, 54514-58, 54560-65, 54615-758, 55186-89, 73298-385, 73519-644, 78822, 79075-461, 79654-79, and CAS 117444-65, from Mutahi, between 1800 and 3600 feet elevation, collected between 10 and 20 May 1966; MCZ 54566-67, 54569-72, 54574-75, 54577-80, 54582, 54584-94, 54596-614, 55190-94, 73633-41, from Melilup, between 3000 and 4000 feet elevation, collected between 12 and 20 May 1966; MCZ 55195-6 from Ramazon River at Melilup, 19 May 1966.

Diagnosis. A moderately large *Batrachylodes,* snout-vent length of mature males measuring about 25 to 32 mm and of mature females 26 to 35 mm (Table 1); dorsal ground color relatively uniform brownish or variously patterned, a dark brownish, dorsally even-margined lateral band on the side of the head, narrowing on the flanks; ratio of interorbital breadth to length of first finger about 1.2 to 1.6, to length of third finger about 0.53 to 0.76, and to length of fourth finger 0.61 to 0.77; disk of first finger scarcely dilated, its diameter 41 to 52 per cent of diameter of third finger disk; diameter of third finger disk usually greater than diameter of tympanum (94 to 130 per cent); diameter of third toe disk 79 to 100 per cent of diameter of second finger disk and 61 to 81 per cent of diameter of third finger disk.

Description. Snout-vent length of 24 females 26.7 to 34.6 mm, of 30 males 24.8 to 32.0 mm (however, several females between 26 and 28 mm in snout-vent are immature, as judged by the straight, undilated oviducts); hindlimbs moderately long, the length of the tibia about 42 to 50 per cent of the snout-vent length;

breadth of head slightly less to slightly greater than length of head, 74 to 87 per cent of length of tibia; eye moderate, its diameter less than length of snout; tympanum distinct, its diameter 49 to 55 per cent of diameter of eye and 94 to 120 per cent of breadth of disk of third finger (Table 3); canthus rostralis rounded; loreal region moderately oblique, slightly concave; tongue with a shallow-rounded or v-shaped notch posteriorly; a low, moderate fold dorsal and posterior to tympanum; fingers without webs; tips of fingers, except for first finger, broadly dilated (the dilation of the disks and the relative lengths of the finger do not differ greatly from the condition exhibited by *B. vertebralis;* Fig. 3, right); diameter of disk of third finger 38 to 48 per cent of length of third finger, ventral pad of disks separated from the dorsal part by a circummarginal groove; first finger shorter than the second which is somewhat shorter than the fourth when adpressed (71 to 84 per cent as measured); subarticular tubercles moderate, oval to round, not strongly protruding; inner metacarpal tubercle large, longer than broad; outer metacarpal tubercle similar but smaller; median tubercle large, oval; toes webbed at base; tips of toes expanded into moderate disks; diameter of disk of third toe about 80 to 100 per cent of diameter of disk of second finger, 61 to 81 per cent of diameter of disk of third finger (Table 3); ventral part of disk separated from dorsal part by a circummarginal groove; subarticular tubercles moderate in size, somewhat more protruding than those of fingers; inner metatarsal tubercle elongate, narrow, oval; outer one round; solar area smooth.

Skin of dorsum and belly is smooth. The posterior thighs are marked by a pattern of low, flattish granules.

Color (in preservative). Dorsal ground color grayish to dark brown, relatively uniform or with varied pattern of lighter or darker markings; a dark brown band with relatively smooth dorsal margin extending from the snout through the eye and tympanum and posteriorly on to the flank. This band usually covers the entire loreal region. Many specimens exhibit a whitish line or series of white spots along the upper margin of the dark, lateral band and variable white spotting of the limbs and dorsum. The undersurface of the hindlimbs and the anterior venter are lightly or heavily speckled with brown.

Measurements of type. Snout-vent length 34 mm; length of head 12.2 mm; breadth of head 13.1 mm; diameter of eye 4.2 mm; diameter of tympanum 2.2 mm; length of snout 4.8 mm; length of hindlimb 51.7 mm; length of tibia 15.8 mm; length of third finger

5.6 mm; diameter of disk of third finger 2.25 mm; diameter of disk of third toe 1.5 mm.

Distribution. Known from the mountains of northern Bougainville Island at elevations from 2000 to 4000 feet.

Comparisons. In size at maturity *B. elegans* is only slightly larger than *B. wolfi,* on the average, and females somewhat smaller than those of *B. montanus.* Other characteristics which distinguish *B. elegans* from *B. vertebralis, B. wolfi,* and *B. gigas* have been discussed in previous sections. *B. elegans* is further differentiated from *B. montanus* by the greater breadth of the interorbital relative to the length of the fingers; the larger tympanum relative to the breadth of the third finger disk, and the greater breadth of the third toe disk relative to the breadth of the second or third finger disks.

Batrachylodes montanus sp. nov.

Holotype. MCZ 55009, an adult female, collected by Fred Parker at Melilup, between 3500 and 4000 feet elevation, on Bougainville Island, Solomon Islands, 19 May 1966.

Paratypes. (all collected by Fred Parker on Bougainville Island) MCZ 55010 (31 May 1966), 73762-3 (31 March 1966), from Lake Loloru, between 4000 and 4300 feet elevation; MCZ 55011, 55013-15, from Melilup, between 3500 and 4000 feet elevation, collected 19 May 1966; MCZ 55529-32, and CAS 117443, from Mutahi, between 3000 and 3600 feet elevation, collected 18 May 1966.

Diagnosis. A large *Batrachylodes,* snout-vent length of mature males ranging from about 27 to 35 mm, of mature females 39 to about 40 mm for the limited sample available (Table 1); diameter of tympanum less than (70 to 91 per cent) breadth of third finger disk; disks of fingers, except for first finger, much more broadly dilated than those of toes, breadth of disk of third toe about 48 to 67 per cent of breadth of disk of third finger, and about 60 to 80 per cent of breadth of disk of second finger; breadth of disk of first finger usually less than 50 per cent of breadth of disk of third finger; interorbital breadth about 40 to 50 per cent of length of third finger, 50 to 60 per cent of length of fourth finger, and 90 to 110 per cent of length of first finger, breadth of disk of third finger about 70 to 100 per cent of interorbital breadth (Table 3); dorsal ground color gray to brown; brownish band on side of head narrow, irregularly margined or broken, usually not extending posterior to the forelimbs.

Description. Snout-vent length of five mature females 38.2 to 39.4 mm, and eight mature males 26.7 to 35 mm (a female measuring 29.4 mm in snout-vent length is immature); hindlimb moderate, length of the tibia from 42 to 47 per cent of the snout-vent length; breadth of head usually slightly greater than length of head, and about 81 to 100 per cent of length of tibia; eye moderate, its diameter 28 to 35 per cent of breadth of head, about equal to or somewhat less than length of snout; tympanum distinct, its diameter about one-third to one-half diameter of eye and 69 to 91 per cent of diameter of disk of third finger (Table 3); canthus rostralis broadly rounded; loreal region moderately oblique, not or but slightly concave; a low fold may or may not be evident dorsal and posterior to the tympanum; fingers without webs; tips, except for first finger, broadly dilated (the dilation of the disks and the relative lengths of the fingers do not differ markedly from the condition exhibited by *B. vertebralis;* see Fig. 3, right); breadth of disk of third finger about 35 to 43 per cent of its length, about 70 to 100 per cent of interorbital breadth and 80 to 97 per cent of length of first finger (Table 3); ventral pad of finger disks separated from dorsal part by a circummarginal groove; first finger shorter than second, which is shorter than fourth when adpressed (about 71 to 81 per cent, as measured); subarticular tubercles moderate, low; inner and middle metacarpal tubercles broadly oval; outer ones narrow elongate; hindlimbs moderately long; toes with minute webs at base; tips of toes dilated into moderate disks; diameter of disk of third toe about 60 to 80 per cent of diameter of second finger disk and about 48 to 67 per cent of diameter of third finger disk (Table 3); ventral part of disk separated from dorsal part by a circummarginal groove; subarticular tubercles moderate, rounded, not strongly protruding; inner metatarsal tubercle large, about twice as long as broad; outer small, round.

Skin of dorsum and venter smooth; posterior surface of thighs with low, rather inconspicuous granules.

Color (in preservative). Dorsal ground color grayish tan to brown, mottled, or frequently with a long, dark hourglass marking or dark chevron in region of forelimbs, along with dark blotches posteriorly; the dark band on the side of the head is narrow, irregularly margined, terminating at the tympanic region, or fading gradually on the flanks; venter marked by scattered, small dark flecks.

Measurements of type. Snout-vent length 38.6 mm; length of head 13.6 mm; breadth of head 14.6 mm; diameter of eye 4.6 mm; length of snout 5.2 mm; interorbital breadth 3.2 mm; diameter of

tympanum 2.1 mm; length of hindlimb 58.3 mm; length of tibia 17.7 mm; length of third finger 7.3 mm; diameter of disk of third finger 2.6 mm; diameter of disk of third toe 1.6 mm.

Distribution. Known from higher elevations; about 3000 to 4000 feet in the mountains at the northern and southern ends of Bougainville Island.

Comparisons. Females of *B. montanus,* based on our limited sample, apparently attain larger size at maturity than any of the other species with the exception of *B. gigas.* It differs from *B. wolfi, B. gigas,* and *B. elegans* in some features of color pattern (see those species). It may be distinguished from *B. elegans, B. vertebralis,* and *B. wolfi* in the greater length of the fingers relative to the interorbital distance, and the smaller tympanum relative to the breadth of the third finger disk. This species also differs from *B. gigas* in the greater breadth of the third toe disk relative to the breadth of the second or third finger disks.

Distributional Pattern

The genus *Batrachylodes* is widely distributed in the Solomons Archipelago, from Buka Island in the north to Santa Ana Island in the south, but surprisingly is unknown from New Ireland, the southernmost island in the Bismarks, about 100 miles from Buka, and is thus apparently endemic to the Solomons.

The evidence as to altitudinal distribution of the genus on the large, northern island of Bougainville, obtained in the present study, indicates that the two large species, *B. gigas* and *B. montanus,* occur only above 3000 feet, the approximate lower limit of the submontane rainforest. *B. elegans* has a somewhat broader montane range, being recorded from elevations as low as about 2000 feet. *B. minutus* has been recorded only from elevations between 1000 and 3000 feet. The species *B. wolfi* and *B. trossulus* have been recorded from sea level to about 4000 feet, as has *B. vertebralis* in southern Bougainville Island. The population of *vertebralis* from the north end of Bougainville is apparently limited to elevations below 3000 to 3500 feet. Also, it should be noted that *B. gigas* is known only from the mountains at the southern end of Bougainville, and *B. elegans* is known only from the mountains at the north end. This interesting distributional pattern for the genus on Bougainville suggests that thorough exploration of the mountain habitats of other of the Solomons islands may well discover other isolated, montane species.

KEY TO THE SPECIES OF *BATRACHYLODES* IN THE SOLOMON ISLANDS

As previously noted, the several large-disked species of this genus, though readily distinguished in the field on the basis of voice characteristics and at times living-color features which disappear in preservative, do not lend themselves to ready identification of individuals by means of a typical dichotomous key. It is hoped, however, that the following key, based on a combination of characters amounting almost to a diagnosis, may serve to distinguish even small samples of adult individuals. Differences in characteristics of juveniles are not yet clear.

1. Tips of fingers only slightly to moderately dilated; breadth of disk of third toe usually greater than to about equal to breadth of disk of third finger; breadth of disk of third finger usually less than 30 per cent (occasionally about one-third) the length of third finger 2
   Tips of fingers moderately to broadly dilated; breadth of disk of third toe usually less than 75 per cent (rarely up to 85 per cent) of breadth of disk of third finger; breadth of disk of third finger greater than 30 per cent of length of third finger 4
2. Size at maturity about 21 to 27 mm in snout-vent length (60 specimens); breadth of disk of third toe about 90 to 125 per cent of breadth of disk of third finger ..... *B. mediodiscus*
   Size at maturity about 15 to 23 mm in snout-vent length (62 specimens); breadth of disk of third toe about 140 to 180 per cent of breadth of disk of third finger 3
3. Size at maturity 15.8 to 19.3 mm in snout-vent length (22 specimens); breadth of head more than 70 per cent of tibia length (Table 2); lateral surfaces without extensive dark band from tip of snout to near groin and on outer surface of thigh (if present, much reduced), usually with broad, dark, transverse bands on hindlimbs ..... *B. minutus*
   Size at maturity 18.1 to 22.7 mm in snout-vent length (40 specimens); breadth of head rarely more than 70 (usually about 65) per cent of tibia length (Table 2); lateral surfaces with prominent blackish band from tip of snout to near groin and on outer surface of thigh; dark, transverse bands on hindlimbs lacking or very faint ..... *B. trossulus*
4. Mature females attaining more than 40 mm in snout-vent length; breadth of disk of third finger about 30 to 40 per cent of length of third finger and usually less than 75 per cent of

length of first finger; interorbital distance about 95 to 100 per cent of length of first finger; uneven-margined, blackish band or large blotches on anterior thigh, inner surface of tibia and under surface of tarsus ..... *B. gigas*
Mature females not attaining more than 40 mm in snout-vent length; breadth of disk of third finger 35 to 55 per cent of length of third finger and usually more than 75 per cent of length of first finger; blackish bands absent from anterior thigh, inner surface of tibia, and under surface of tarsus 5

5. Snout-vent length of mature females between 30 to 40 mm; interorbital distance less than 60 per cent of length of fourth finger and 90 to 110 per cent of length of first finger; tympanum usually less than 90 per cent of breadth of third finger disk; breadth of third toe disk 48 to 65 per cent of breadth of third finger disk ..... *B. montanus*
Snout-vent length of mature females between 24 and 35 mm; interorbital distance usually greater than 60 per cent of length of fourth finger, and usually greater than 110 per cent of length of first finger; breadth of third toe disk 55 to 85 per cent of breadth of third finger disk 6

6. Snout-vent length of 40 mature males about 21 to 28 mm, of 30 mature females 24 to 29 mm; dark band on side of head usually confined to upper loreal region, rather uneven-margined dorsally, terminating at point anterior to forelimbs or, if extending on to the flank, usually with a break or deep indentation just anterior to the forelimb; breadth of head about 70 to 80 per cent of length of tibia (only for population from northern Bougainville Island); interorbital breadth less than 60 per cent of length of third finger, and usually less than 120 per cent of length of first finger (only for population from northern Bougainville Island) ..... *B. vertebralis*
Snout-vent length of 50 mature males 25 to 32 mm, of 44 mature females 27 to 32 mm; dark band on side of head usually even-margined dorsally (often covering most of loreal region for *B. elegans*), and usually without break or indentation anterior to forelimb; breadth of head about 75 to 95 per cent of length of tibia; interorbital breadth usually greater than 60 per cent of length of third finger and usually greater than 130 per cent of length of first finger 7

7. Dorsal ground color greenish to olive (dark brown in melanistic individuals), relatively uniform; lateral band blackish (at least in life); interorbital distance 73 to 92 per cent of length

of fourth finger length of first finger 55 to 67 per cent of length of fourth finger; disk of first finger distinctly dilated and breadth of its disk usually greater than 50 per cent of breadth of third finger disk ..... *B. wolfi*
Dorsal ground color tan or brown, variously marked with darker or lighter patterns; lateral band dark brown; interorbital distance about 60 to 77 per cent of length of fourth finger; length of first finger 48 to 60 per cent of length of fourth finger; disk of first finger scarcely dilated and breadth of its disk usually less than 50 per cent of breadth of third finger disk ..... *B. elegans*

ACKNOWLEDGEMENTS

We are indebted to Dr. Ernest Williams, Museum of Comparative Zoology, for suggesting that we review this genus. We are also indebted to Dr. Alice Grandison, British Museum of Natural History, for the opportunity of examining the type of *Batrachylodes vertebralis,* and to Dr. Konrad Klemmer, Senckenberg Museum, for the opportunity of examining the type of *Sphenophryne wolfi* (=*Batrachylodes wolfi*). This study is part of the senior author's program concerned with the herpetofaunas of the Pacific Islands. The program has been supported by National Science Foundation grants No. GB-409 and No. GB-4156; the collection and curating of the material was partly supported by National Science Foundation grant GB-6944 to Ernest E. Williams. Illustrations were prepared by Mr. Walter Zawojski, Stanford University.

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(Received 18 November 1969.)

TABLE 1

Size at maturity of the species of *Batrachylodes* known from the Solomon Islands (R=range, M=mean, N=number)

	Snout-vent length at maturity	
	Male	*Female*
Batrachylodes minutus	R=15.8-17.7 M=16.9 N=6	R=16.7-19.3 M=17.8 N=16
Batrachylodes trossulus	R=18.1-20.8 M=19.4 N=20	R=18.1-22.7 M=20.7 N=20
Batrachylodes mediodiscus	R=21.6-25.8 M=23.7 N=22	R=21.7-27.0 M=24.2 N=20
Batrachylodes wolfi	R=25.2-30.6 M=27.7 N=20	R=28.2-31.9 M=29.9 N=20
Batrachylodes vertebralis (north end of Bougainville)	R=21.6-26.7 M=24.3 N=22	R=24.1-27.6 M=26.06 N=20
Batrachylodes vertebralis (south end of Bougainville)	R=21.4-28.6 M=26.08 N=18	R=25.4-29.5 M=27.36 N=5
Batrachylodes elegans	R=24.8-32.4 M=29.1 N=30	R=26.7-34.6 M=30.5 N=24
Batrachylodes gigas	R= M= N=	R=42.7-46.0 M=44.47 N=3
Batrachylodes montanus	R=26.7-35.4 M=32.6 N=8	R=38.2-39.4 M=38.6 N=5

TABLE 2

Pertinent proportional differences for species of *Batrachylodes* with small finger disks (R=range, M=mean, N=number)

	Breadth of disk of 3rd finger / *Length of 3rd finger*	*Breadth of disk of 3rd toe* / *Breadth of disk of 3rd finger*	*Length of 3rd finger* / *Breadth of head*	*Breadth of head* / *Length of tibia*
Batrachylodes minutus	R=0.143-0.238 M=0.198 N=16	R=1.38-2.33 M=1.83 N=16	R=0.318-0.380 M=0.348 N=16	R=0.697-0.855 M=0.763 N=20
Batrachylodes trossulus	R=0.143-0.240 M=0.188 N=20	R=1.42-2.28 M=1.79 N=20	R=0.340-0.452 M=0.397 N=20	R=0.618-0.725 M=0.654 N=20
Batrachylodes mediodiscus	R=0.231-0.345 M=0.292 N=20	R=0.900-1.25 M=1.07 N=20	R=0.299-0.372 M=0.325 N=20	R=0.664-0.791 M=0.742 N=20

TABLE 3

Pertinent proportional differences for samples of species of *Batrachylodes* with larger finger disks (R=range, M=mean, N=number)

	Batrachylodes wolfi	*Batrachylodes elegans*	*Batrachylodes gigas*	*Batrachylodes vertebralis* (south end of Bougainville)	*Batrachylodes montanus*
Breadth of disk of 3rd toe / Breadth of disk of 2nd finger	R=0.722-1.00 M=0.861 N=20	R=0.789-1.00 M=0.888 N=20	R=0.909-0.950 M=0.933 N=5	R=0.714-0.869 M=0.780 N=20	R=0.595-0.800 M=0.716 N=10
Breadth of disk of 3rd toe / Breadth of disk of 3rd finger	R=0.650-0.867 M=0.710 N=20	R=0.611-0.812 M=0.704 N=20	R=0.714-0.833 M=0.773 N=5	R=0.555-0.742 M=0.659 N=20	R=0.482-0.646 M=0.561 N=12
Breadth of disk of 3rd finger / Interorbital breadth	R=0.517-0.833 M=0.660 N=20	R=0.583-0.772 M=0.664 N=20	R=0.582-0.747 M=0.670 N=20	R=0.640-0.860 M=0.720 N=20	R=0.696-1.00 M=0.827 N=13

Interorbital breadth / Length of 3rd finger	R=0.579-0.725 M=0.654 N=20	R=0.529-0.762 M=0.641 N=20	R=0.474-0.539 M=0.511 N=5	R=0.489-0.574 M=0.528 N=20	R=0.429-0.565 M=0.482 N=13
Interorbital breadth / Length of 1st finger	R=1.16-1.50 M=1.34 N=20	R=1.16-1.59 M=1.40 N=20	R=0.946-1.02 M=0.981 N=5	R=1.07-1.25 M=1.16 N=20	R=0.900-1.12 M=1.02 N=13
Interorbital breadth / Length of 4th finger	R=0.732-0.915 M=0.803 N=20	R=0.616-0.773 M=0.681 N=20	R=0.574-0.611 M=0.586 N=5	R=0.577-0.689 M=0.625 N=20	R=0.484-0.632 M=0.556 N=12
Diameter of tympanum / Breadth of disk of 3rd finger	R=0.706-1.20 M=0.905 N=20	R=0.939-1.20 M=1.05 N=20	R=0.833-1.11 M=0.963 N=5	R=0.811-1.24 M=0.947 N=20	R=0.692-0.913 M=0.778 N=11
Diameter of eye / Breadth of head	R=0.306-0.385 M=0.339 N=20	R=0.308-0.376 M=0.334 N=20	R=0.298-0.347 M=0.323 N=5	R=0.330-0.396 M=0.365 N=20	R=0.289-0.378 M=0.336 N=12

TABLE 3 — (continued)

	Batrachylodes wolfi	*Batrachylodes elegans*	*Batrachylodes gigas*	*Batrachylodes vertebralis* (south end of Bougainville)	*Batrachylodes montanus*
Length of 2nd finger / Length of 4th finger	R=0.771-0.882 M=0.824 N=20	R=0.718-0.842 M=0.782 N=20	R=0.683-0.766 M=0.717 N=5	R=0.706-0.831 M=0.753 N=20	R=0.710-0.811 M=0.758 N=12
Breadth of disk of 3rd finger / Length of 1st finger	R=0.750-1.04 M=0.878 N=20	R=0.750-1.05 M=0.922 N=20	R=0.648-0.747 M=0.658 N=5	R=0.737-0.944 M=0.825 N=20	R=0.786-0.968 M=0.870 N=12
Breadth of disk of 1st finger / Breadth of disk of 3rd finger	R=0.500-0.611 M=0.561 N=20	R=0.417-0.526 M=0.468 N=20	R=0.500-0.625 M=0.568 N=20	R=0.424-0.533 M=0.470 N=20	R=0.407-0.526 M=0.466 N=12
Breadth of disk of 3rd finger / Length of 3rd finger	R=0.368-0.546 M=0.415 N=20	R=0.341-0.476 M=0.418 N=20	R=0.316-0.394 M=0.347 N=5	R=0.340-0.411 M=0.380 N=20	R=0.356-0.435 M=0.398 N=13

Length of 3rd finger / Head length	R=0.355-0.446 M=0.397 N=20	R=0.379-0.435 M=0.403 N=20	R=0.414-0.461 M=0.431 N=5	R=0.390-0.472 M=0.435 N=20	R=0.423-0.537 M=0.492 N=12
Length of tibia / Snout-vent Length	R=0.375-0.468 M=0.426 N=20	R=0.420-0.508 M=0.466 N=20	R=0.444-0.522 M=0.481 N=20	R=0.400-0.488 M=0.465 N=20	R=0.424-0.489 M=0.449 N=12
Breadth of head / Snout-vent length	R=0.328-0.399 M=0.378 N=20	R=0.334-0.404 M=0.375 N=20	R=0.364-0.415 M=0.389 N=5	R=0.356-0.397 M=0.369 N=20	R=0.362-0.416 M=0.385 N=12
Breadth of head / Length of tibia	R=0.825-0.947 M=0.873 N=20	R=0.740-0.868 M=0.806 N=20	R=0.733-0.889 M=0.807 N=5	R=0.741-0.894 M=0.831 N=20	R=0.788-0.975 M=0.862 N=12

TABLE 4

Proportional differences for samples of *B. vertebralis* from the northern and southern ends of Bougainville Island

(R=range, M=mean, N=number)

	Interorbital breadth / *Diameter of eye*	*Interorbital breadth* / *Length of 3rd finger*	*Interorbital breadth* / *Length of 4th finger*	*Length of 1st finger* / *Length of 4th finger*	*Length of 1st finger* / *Length of 3rd finger*	*Interorbital breadth* / *Snout length*	*Interorbital breadth* / *Length of head*
Batrachylodes vertebralis (north end of Bougainville)	R=0.682-0.897 M=0.788 N=20	0.542-0.743 0.651 20	0.635-0.933 0.791 20	0.533-0.704 0.610 20	0.444-0.543 0.498 20	0.637-0.867 0.746 20	0.247-0.314 0.285 20
Batrachylodes vertebralis (south end of Bougainville)	R=0.568-0.697 M=0.627 N=20	0.489-0.574 0.528 20	0.577-0.689 0.625 20	0.487-0.595 0.547 20	0.404-0.489 0.455 20	0.535-0.667 0.603 20	0.205-0.249 0.231 20

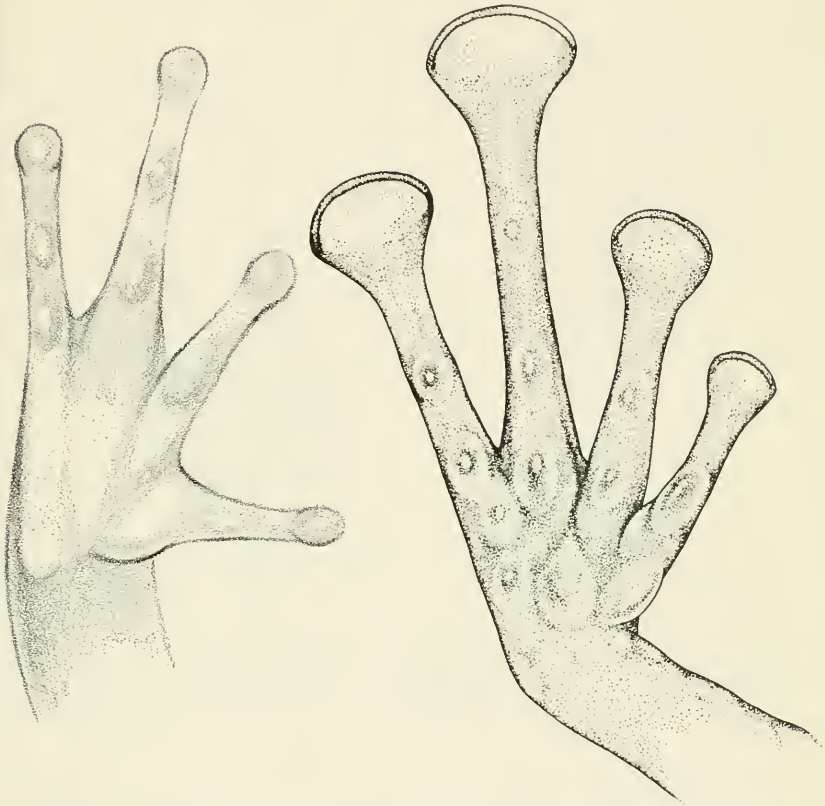

FIG. 1. (to contrast large disked and small disked species) Left: *Batrachylodes trossulus,* inferior view of hand. Right: *B. gigas,* inferior view of hand.

FIG. 2. Left: *Batrochylodes minutus*, inferior view of hand. Right: *B. mediodiscus*, inferior view of hand.

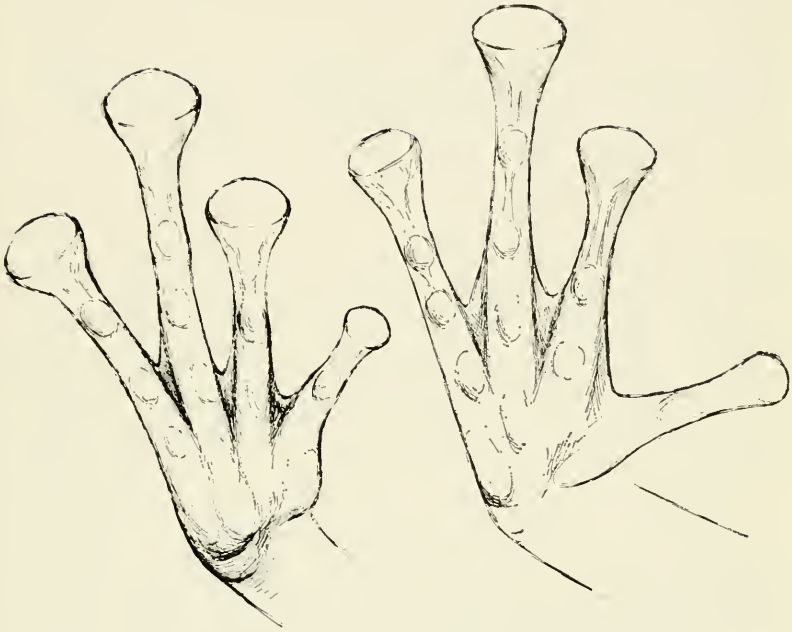

FIG. 3. Left: *Batrachylodes wolfi*, inferior view of hand. Right: *B. vertebralis*, inferior view of hand.

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CAMBRIDGE, MASS. 3 APRIL, 1970 NUMBER 347

DESCRIPTION, OSTEOLOGY AND RELATIONSHIPS OF THE AMAZONIAN CYPRINODONT FISH *FLUVIPHYLAX PYGMAEUS* (MYERS AND CARVALHO)

Tyson R. Roberts[1]

ABSTRACT. The minute Amazonian cyprinodontid *Fluviphylax pygmaeus* (Myers and Carvalho) is redescribed and its osteology worked out based on material obtained by the Expedição Permanente da Amazônia (EPA). Its relationships apparently lie either with the Procatopodinae (a subfamily otherwise restricted to Africa) or with the Fundulinae, and not with the Rivulinae. A new subfamily, Fluviphylacinae, is proposed for it. The very smallest egg-laying and live-bearing cyprinodonts occur in Amazônia, whereas the largest ones are found in habitats geographically or ecologically isolated from rich fish faunas.

ACKNOWLEDGEMENTS

I wish to thank Prof. George S. Myers, Division of Systematic Biology, Stanford University, and Dr. Neal R. Foster, Department of Limnology, Academy of Natural Sciences of Philadelphia, for critically reviewing the manuscript of this paper and offering helpful suggestions.

INTRODUCTION

This paper deals with an almost unknown but widely distributed Amazonian cyprinodontid fish of minute size, *Fluviphylax pygmaeus* (Myers and Carvalho). Prof. George S. Myers of Stanford University kindly supplied the following information about its original discovery. In 1942-44, when Myers was working at the Museu Nacional in Rio de Janeiro in collaboration with Sr. Antenor Leitão de Carvalho, Naturalista of the Museu, a man named Alexandre Parko was collecting for the Museu in Amazonia. Although primarily concerned with insects, Parko obtained a few vertebrates, including the type of a remarkable toad, *Bufo dapsilus* Myers and

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Carvalho (1945a), from Benjamin Constant, and the type of a strange, leaf-nosed lizard, *Anolis phyllorhinus* Myers and Carvalho (1945b), from Borba on the lower Rio Madeira.

The Parko material from Borba also included specimens of a remarkable new genus and species of minute cyprinodontid with enormous eyes, obviously closely related neither to *Rivulus* nor to any other previously described South American member of the family. Myers already had been aware that a cyprinodontid of this type existed in Amazonas; as a student under the late Prof. Carl H. Eigenmann he had found one partially squashed and otherwise poorly preserved specimen from the lower Rio Amazonas while unpacking fishes collected by the late Carl Ternetz in 1923-25. This specimen was in no condition for description and seems eventually to have become lost. Carvalho and Myers planned to describe the Parko specimens, but Myers had to leave Rio before this was done, bringing with him to Stanford only three specimens. Later, when Carvalho was at Stanford on a Guggenheim Fellowship, some more work was done on the fish, and Carvalho prepared a drawing of it. Unfortunately the drawing and data were lost in the late 1950's.

While preparing a resumé of cyprinodontid subfamilies, Myers (1955) gave a brief diagnosis of Parko's tiny Amazonian fish, which now may be reproduced:

> One new fish that aquarists will probably see before too long is the very tiny *Potamophylax pygmaeus* Myers and Carvalho, from the Middle Amazon. It is one of the smallest of all killies, and its place in the above classification is not clear. The strange characteristics, as worked out by Mr. Carvalho and me, include enormous eyes, a dorsal fin set entirely behind the anal fin, high-set pectoral fins and a deep "pocket" beside the latter fin. It represents a hitherto unknown genus and species and it may be related to the African lampeyes.

Although no type specimens were designated, the description satisfied the rules of zoological nomenclature in effect at the time it was published, and therefore is nomenclaturally valid. Whitley (1965: 25) pointed out that *Potamophylax* Myers and Carvalho is preoccupied by *Potamophylax* Wallengren, 1891 (a neuropteran insect), and proposed the substitute name *Fluviphylax,* with *P. pygmaeus* as type species. The species apparently never has been imported as an aquarium fish and nothing further has been reported about it.

Since the types are few in number and only in fair condition, it

was highly desirable to obtain more material. In 1968 I participated in field work in Amazonas as a member of the Expedição Permanente da Amazônia. EPA is a continuing, cooperative effort among the Museu Goeldi in Belem, the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus, and the Museu de Zoologia of the Universidade de São Paulo (MZUSP),[1] financed by the Fundação de Amparo à Pesquisa of the state of São Paulo. I wish to thank Dr. P. E. Vanzolini, Director of the Museu de Zoologia, for arranging my participation. September 20 through November 5 we worked on the Rio Solimões between Manaus and Santo Antonio do Içá (the Middle Amazon). The scientific party consisted of Heraldo A. Britski (leader), Júlio Cesar de Garavello, Silvia Gerken, Naercio A. Menezes and myself. Our primary purpose was to collect fishes and we were fortunate in obtaining *Fluviphylax* at several localities. The extensive collections from this trip are being sorted at the Museu de Zoologia. Additional *Fluviphylax* were located in the material obtained by EPA on the Lower Amazon in 1967 (its first year in operation). With the kind permission of Heraldo Britski, who is in charge of the fish collections, I brought two lots to the United States for this study. Finally, it is of considerable interest to note that the Museum of Comparative Zoology has a few small lots of *Fluviphylax* obtained by the Thayer Expedition under Louis Agassiz in 1866. In all probability Garman had the Agassiz specimens in hand when he wrote his monograph, "The Cyprinodonts" (Garman, 1895), but passed them over as the young of *Rivulus*.

Since they are liable to be confused, care has been taken to distinguish *Rivulus* from *Fluviphylax* in the following generic characterization. The easiest distinctions to use involve eye size, nature of orbital rim, number of suborbital scale rows, width of head, condition of anterior nostril, jaw structure, and relative positions of pectoral and pelvic fins.

Genus FLUVIPHYLAX Whitley

Potamophylax Myers and Carvalho, in Myers, 1955: 7 (original description: type species *P. pygmaeus* Myers and Carvalho, by original designation; name preoccupied by *Potamophylax* Wallengren, 1891, a neuropteran insect).

[1] Formerly Departamento de Zoologia of the Secretaría da Agricultura of the state of São Paulo. The name was changed in June, 1969, when it became part of the Universidade de São Paulo.

Fluviphylax Whitley, 1965: 25 (replacement name for *Potamophylax* Myers and Carvalho, and therefore taking same monotype).

Characteristics. Tiny egg-laying cyprinodonts, widespread in Amazonas, typically found in still backwaters. Largest specimen available for measurement 18.5 mm; females as small as 14.5 mm with ripe ovaries.[1] Body moderately elongate, sub-cylindrical in cross-section, sides not compressed. Body axis straight. Head about as wide as deep (head considerably wider than deep in *Rivulus*). Eye extremely large, nearly as deep as head, its dorsal margin either flush with dorsal contour of head or barely below it, and largely exposed dorsally (supraorbital portion of frontal bone only partially covering eye); orbital rim free (eye of moderate size, covered dorsally, and with attached orbital rim in *Rivulus*). Preorbital space narrow, about .25 diameter of eye. Interspace between eye and upper angle of preopercle extremely narrow; preopercular segment of cephalic sensory canal system very close to posterior margin of eye. A single row of scales extending just below eye. Below this suborbital scale row the interopercle can be lifted sideways to reveal a deep furrow in the skin separating geniohyoideus muscles from jaw suspension (there are at least two or three suborbital scale rows in *Rivulus,* and the area between geniohyoideus muscles and jaw suspension is smooth and scaled over). Snout short, about .5 eye diameter, its dorsal contour with a slight concavity anterior to eye. Anterior nasal opening a pore flush with snout (tubular in *Rivulus*). All segments of cephalic sensory canal usually open, but a few specimens have one or more of the segments closed. Some scales of midlateral series with pit organs. Mouth small, superior, the small upturned jaws set at an angle of about 45 degrees (mouth less superior in *Rivulus,* with a very characteristic, deep, right-angled notch or recess between nasal and lacrimal bones into which rictal membranes fit). Jaw teeth conical, in two irregular rows in both jaws, teeth of outer and inner rows of about the same size. Tongue free from floor of mouth for most of its length; rounded in cross-section near the tip, posteriorly a somewhat flattened triangle in cross-section (with apex downward and lying between left and right m. geniohyoidei) (in *Rivulus* tongue attached to floor of mouth except for its anterior third, flattened in cross-section throughout its free portion, and broadly rounded or blunt at tip). No teeth on palate (prevomer usually bearing teeth in *Rivulus*). Intestine in anterior third of body forming one and a

[1] Standard lengths only are recorded in this paper.

half vertical loops at an angle of about 30 degrees to body axis (anterior portion of looping to left and posterior portion to right side of body); straight in remaining two-thirds of body cavity. Stomachs of numerous specimens contain minute insect larvae. Gill rakers smooth, slender shafts, widely set, ten on lower and two or three on upper limb of first gill arch. Pseudobranch an ovoid, bilobate, white, glandlike mass without filaments about .5 mm high in a 16-mm specimen, covered by a transparent membrane. Origin of gill opening about .25 eye diameter in front of pectoral fin base, on a level with or slightly below origin of uppermost pectoral ray. Gill membranes free from isthmus, united to each other at a point on a vertical with posterior margin of eye. Branchiostegal rays usually five on either side.

Dorsal fin small, with five or six rays, its origin distinctly posterior to a vertical line through base of last anal ray (dorsal fin set equally far back in some species of *Rivulus,* but usually with more rays). Anal fin much larger than dorsal, with eight or nine rays. Anal fin pterygiophores slender except for the first, which is moderately expanded. Caudal fin rounded. Pectoral fins high-set, uppermost pectoral ray originating distinctly above lateral midline of body, and extending well beyond base of pelvic fin (uppermost pectoral ray inserted below midline in *Rivulus,* and pectoral fin failing to reach pelvic base). Internal to base of pectoral fin a deep pocket, the entrance to which is guarded by delicate tissues easily ruptured (similar pockets present in all cyprinodonts). Pelvic fins separate, not connected by membrane, with six rays. Pelvic insertion equidistant between origin of lowermost pectoral ray and anal fin origin.

In mature males dorsal, pelvic, and anal rays slightly to moderately elongated, and dorsal, pelvic, anal and caudal fins with a barred pattern (strongest on anal and caudal). Shape of caudal fin unaffected by sexual dimorphism. Examination of scales and fins with direct and transmitted light failed to reveal contact organs. Ripe females contain 30-40 eggs, the largest of which are somewhat over .1 mm in diameter, and their abdomens are slightly distended (best seen viewing specimen from above). Teasing the surface of eggs isolated from the ovary reveals elongate chorionic filaments which apparently originate from a restricted portion of the chorion, but no short, spinelike projections (short, spinelike projections are distributed over the entire chorionic surface in various atherinoids, *Oryzias* and *Horaichthys*). Ovary single, without indication of division between right and left halves. Males with cloacal-genital area unswollen, a small, distinctly tubular opening

to sperm duct slightly in advance of base of first anal ray. Some females with cloacal-genital area considerably swollen, an oviducal pouch opening in front of first anal ray (the membranes of this pouch do not encroach upon first anal ray, nor do they extend along side of anal fin base, as happens in some Fundulinae).

Fluviphylax pygmaeus (Myers and Carvalho)
Figures 1 and 2

Potamophylax pygmaeus Myers and Carvalho, in Myers, 1955: 7 (original description; type locality "Middle Amazon"=Borba, lower Rio Madeira; types in Museu Nacional, Rio de Janeiro; three paratypes at Stanford).

Fluviphylax pygmaeus Whitley, 1965: 25 (name only).

Material studied. SU 50196, three paratypes 14.9-16.1 mm, Rio Madeira at Borba, collected in 1943 by A. Parko; MZUSP 6245, 13 specimens 11.5-18.5 mm, "lago above Manaus," margem esquerda Rio Negro, Amazonas, Brasil, collected by EPA April 28, 1967; MZUSP 5590, 50 specimens 9.9-17.0 mm, Lago Parauacui, near Oriximina, Pará, Brasil, February 9, 1967, EPA; MCZ 41367, five specimens 12.9-14.4 mm, Lago Hyanuary, Amazonas, Brasil, 1865-66, Thayer Expedition; MCZ 6262, five specimens 10.3-10.5 mm, Obidos, Pará, Brasil, 1865-66, Thayer Expedition; MCZ 6265, one specimen 12.9 mm Lago Alexo,[1] Amazonas, Brasil, 1865-66, Thayer Expedition.

[1] In response to my inquiry, Prof. Myers provided the following information about this locality:

Many Thayer Expedition fishes came from Lago Alexo. The name may be misspelt, as are some other Thayer localities. It may have been "Lagôa Aleixo." However, there is no such place listed, spelt either way, in the 4 volumes of Pinto's "Diccionario Geographico," including the several little addenda at the ends of the volumes. "Journey in Brazil," the narrative of the Thayer Expedition by Louis and Mrs. Agassiz, has no index and does not give a complete itinerary of the separate trips made by expedition members in the Amazon. However, on p. 294, it records the return of Thayer to Manaus on December 6, 1865. Going backward in the book, the last previous mention of Thayer is on p. 282, where it says that he and Bourget were sent (from Manaus) to "Lake Cudajas, to be gone ten days," this being recorded under the date of November 20. That is, unless two separate small trips were involved, which is doubtful, Thayer started for "Lake Cudajas" on November 20 and "returned from Lago Alexo" 16 days later. "Lago Alexo" may be the same as "Lake Cudajas," the correct name of which Thayer could have found to be "Lago Alexo" once he got there. In any event, Lago Alexo cannot be far from Manaus.

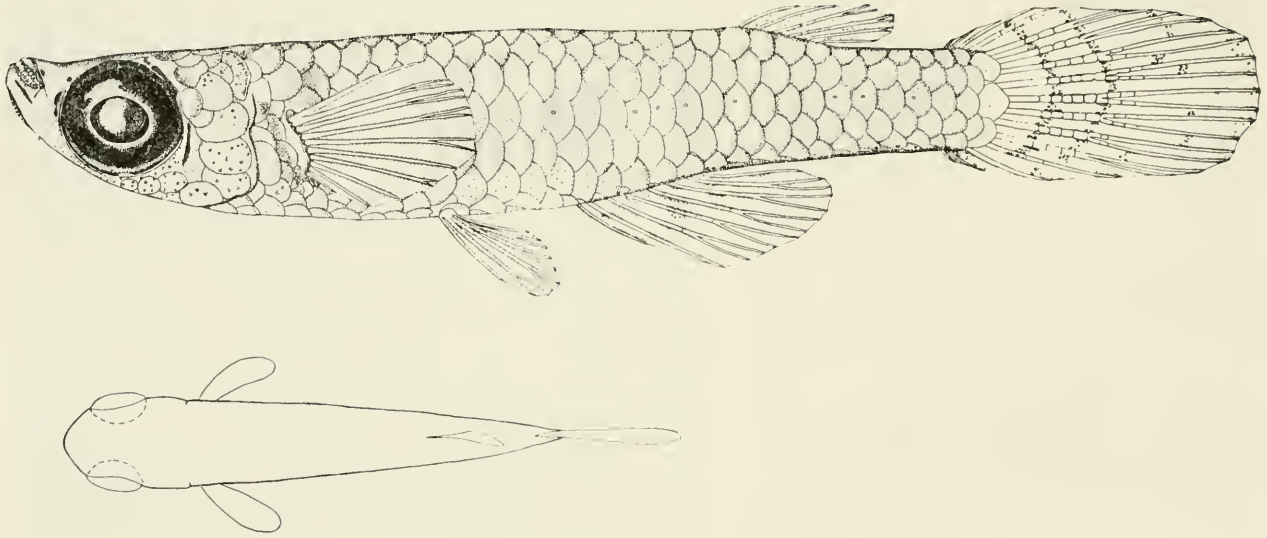

Fig. 1. *Fluviphylax pygmaeus* (Myers and Carvalho). Outline of body, scales, and fins based on alizarin preparation of 18.5-mm male specimen from MZUSP 6245; color pattern, cephalic sensory canals and other superficial features based on slightly smaller specimens from same locality. Inset: dorsal outline.

Morphometric data has not been assembled because superficial examination of the specimens reveals no proportional variations of consequence and because accurate measurements of the small specimens are difficult. The proportions given in the following description were obtained by measurements on a few specimens or by stepping off distances with a pair of dividers and are meant to provide a general impression. Counts of fin rays and scales made on many of the specimens reveal little variation; pectoral, dorsal and anal fin counts vary by only a ray or two.

Body proportions. Greatest depth of body 5.0. Least depth of caudal peduncle 9.0. Head 4.0. Eye 2.5 in head. Bony interorbital space slightly greater than eye diameter. Snout about .5 eye diameter. Width of mouth about .75 interorbital space. Dorsal fin about same size as pelvic fin, length of dorsal fin base about equal to length of base of first five anal rays. Anal fin far larger than dorsal fin, and slightly larger than pectoral fin. Caudal fin distinctly larger than anal fin. Length of caudal peduncle about equal to anal fin base.

Fin rays. Dorsal fin with five or six rays; anal fin usually with eight rays, sometimes nine; in alizarin specimens first two and last two rays of dorsal and anal fins simple, other rays branched. Pectoral fin with 10 or 11 rays, pelvic fin with six rays, caudal fin usually with 17 rays (counts on alizarin preparations reveal eight principal, five upper and four lower procurrent caudal fin rays). Rays in all fins without unusual specializations.

Squamation. Scales uniformly cycloid, 25 or 26 in midlateral series. Anteriorly three, slightly posterior to anal origin two, and on caudal peduncle one, rows of scales between midlateral and dorsomedian scale rows. About 18 or 19 scales in median predorsal series from occiput to origin of dorsal fin. Nine scales around caudal peduncle. Seven scales in diagonal series from in front of dorsal fin origin to middle of anal fin base. About five scales along anal fin base. Fins themselves scaleless except for two rows of normal-sized scales extending beyond hypural fan onto proximal portion of caudal fin. Scales on either side of genital region unenlarged and unspecialized.

I tentatively interpret the squamation on the dorsum of the head in *Fluviphylax* (Fig. 2) as typically consisting of a single *h scale,* a single *g scale* (which overlaps the *e scales* in some specimens but not in others), two *e scales,* two *d scales,* and a single *a scale.* Perhaps owing to the exceptionally large eyes, the *a scale* appears to be further forward than usual. Some specimens appear to have two

scales in the "a" position. Some specimens have a small scale anterior to the *h scale.* There are a pair of scales on either side of the head over the supraorbital portion of the frontal bone. This is a simplified pattern similar to that probably found in many unrelated

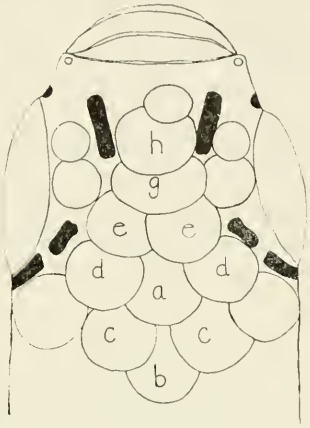

Fig. 2. Scale pattern on dorsum of head in 15.1-mm specimen.

forms in which the pattern has been secondarily reduced, including *Epiplatys sexfasciatus,* young *Nothobranchius* (or *Aphyosemion*?) *sjoestedti,* and perhaps young *Pantanodon podoxys* (Whitehead, 1962, figs. 12 and 13).

Coloration. The MZUSP lots (including several not listed above) I have examined vary from those in which the specimens are relatively dark and have markings that stand out to others in which the specimens are quite pale and the markings are washed out. I am fairly confident, however, that all represent the same species. The coloration is sexually dimorphic. In females in all lots there is a more or less sharp demarcation between the relatively dark sides and the light belly, while the fins are clear or slightly dusky, but never have distinct markings. In males, on the other hand, the body is more uniformly colored, the belly about the same color as the sides; the sides usually bear a series of hazy, lozenge-shaped, vertical bars, from two or three restricted to the pectoral region to a dozen or so for the length of the body; the dorsal, anal and caudal fins bear concentrations of melanophores (see Fig. 1).

Scant observations were made on coloration in live *Fluviphylax* during the EPA fieldwork in which I participated, since all were

taken during rotenone collecting and were seen but briefly before they had to be preserved. I distinctly recall that they lack the shimmering bluish-greenish reflections on the sides possessed by African Procatopodinae such as *Poropanchax rancureli* and *Aplocheilichthys shiotzi*. The most striking feature of their coloration is a silvery sheen, presumably guanin, on the entire dorsal surface of the eyes. As a little *Fluviphylax* swims along just below the water's surface, two brilliant silvery dots (surprisingly large considering the size of the fish) are seen moving along.

Sex ratios. In some MZUSP lots almost all intermediate-sized specimens bear eggs, the smallest specimens are quite evidently immature, and only a few of the largest individuals are males. This suggests they might be protogynous hermaphrodites. In other lots, however, nearly half of the specimens, including ones as small as 12.5-14 mm, are males.

ECOLOGY

Fluviphylax has been collected along large stretches of the Lower and Middle Amazon, and presumably occurs in suitable habitats throughout the Amazon basin. I remember catching a single specimen near the mouth of the Rio Jauaperi, well up on the Rio Negro, but the specimen was lost before it could be preserved. *Fluviphylax* lives in still, shaded, black- or brown-tinted, shallow backwaters, not in the main rivers or even in small, flowing streams. Most fishes in such places are small species. The principal predaceous kinds are likely to be a pair of "dwarf" species of *Acestrorhynchus, A. nasutus,* and *A. minimus,* and occasionally *Hoplias, Hoplerythrinus,* or *Potamorrhaphis.* In EPA collections *Fluviphylax* also is associated with *Crenuchus, Curimatopsis,* several species of *Hemigrammus* and *Hyphessobrycon, Iguanodectes, Hypopomus,* a minute species of *Trichomycterus,* two or three species of *Apistogramma, Cichlasoma festivum,* two tiny species of *Microphilypnus, Poecilia* (*Pamphorichthys*) *minor,* and other small species. *Rivulus* also occurs together with *Fluviphylax,* but my impression is that *Fluviphylax* tends to stay in more open water than *Rivulus,* which during the dry season is likely to be left in small pools that are drying up. *Rivulus* frequently occurs singly in water only inches deep and probably spends long periods relatively motionless, whereas *Fluviphylax* is usually over deeper water and possibly maintains small schools near the surface. Stomach contents of numerous specimens contain minute insect larvae or adults (no other food items observed).

Fluviphylax is evidently the smallest known oviparous cyprinodont. In all sizable samples obtained by EPA (representing the months of February-April and September-October) small specimens predominate, despite probable sampling errors favoring larger specimens. This indicates that reproduction occurs throughout much of the year, perhaps year-round. If so, the bulk of the population probably is sexually immature at all times, and I would not be surprised if the average size of an individual in these populations falls between 9 and 11 mm. If we can judge from other small oviparous cyprinodonts, hatchlings are probably between 4 and 6 mm.

OSTEOLOGY

Figures 3-13 (Reduced to same scale.)

This account of the osteology of *Fluviphylax* is based on four specimens (11.5, 14.4, 16.5 and 17.0 mm) from the MZUSP 5590 and two specimens (17.8 and 18.5 mm) from MZUSP 6245. The figures are based on the larger two of the four specimens from MZUSP 5590. All statements which follow were based on observations verified in at least two or three specimens. The 11.5 mm specimen is well ossified; differences noted between it and larger specimens are 1) failure of nasal bones to ossify; 2) less development of anterolateral parasphenoid wings; and 3) presence of a sixth branchiostegal ray on left side. No osteological differences attributable to secondary sexual dimorphism were detected.

Braincase (Figs. 3-5). Braincase typically cyprinodontoid in appearance (*cf.* numerous figures of cyprinodont crania in dorsal view in Rosen and Bailey, 1963). Cranium very slightly tapered anteriorly. Supraorbital processes of frontal well developed; frontals with a concavity behind supraorbital process for reception of dermosphenotic, which lies over sphenotic and snugly against frontal. Mesethmoid a thin ossification folded back on itself at its anterior margin to form a double lamina open posteriorly. Mesethmoid not contacting prefrontals. Prevomer, parietals, and basisphenoid bones absent. Anterolateral parasphenoid wings moderately developed, not contacting pterosphenoids to form posterior myodomes (in cyprinodonts anterolateral parasphenoid processes play the role corresponding to that of the basisphenoid in other fish groups). Dorsal border of foramen magnum formed exclusively by exoccipital bones. Supraoccipital bone typically cyprinodontoid in form. Exoccipitals and epiotics without posteriorly-directed processes or wings. Supraoccipital with a close-set pair of short

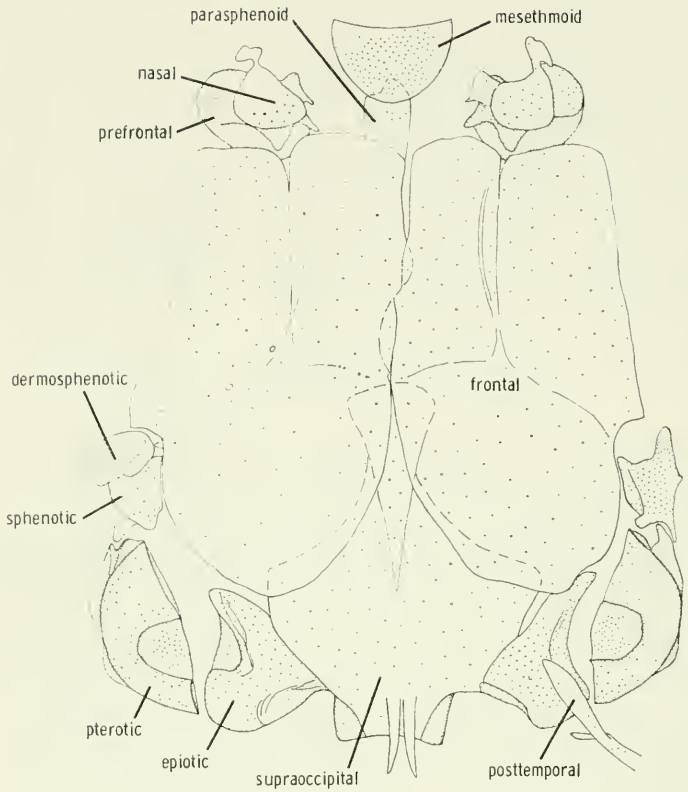

Fig. 3. Dorsal view of cranium, 16.5-mm specimen (all osteological figures based on specimens from MZUSP 5590).

spines extending straight back near dorsal midline. Basicranium with a basioccipital and two exoccipital condyles (Fig. 5). Ventral surfaces of pterotic and sphenotic bones with well-developed sockets for articulation of hyomandibular bone (Fig. 4).

Facial bones (Figs. 6, 7). Nasal bone small and weakly ossified. Lacrimal bone weakly ossified, its shape seemingly determined solely by its function as a bony trough for preorbital segment of cephalic sensory canal system and its relation to anterior margin of eye. Bony trough in upper arm of preopercle for postorbital segment of cephalic canal system extremely close to hind border of eye. Bony troughs for segments of cephalic canal system formed

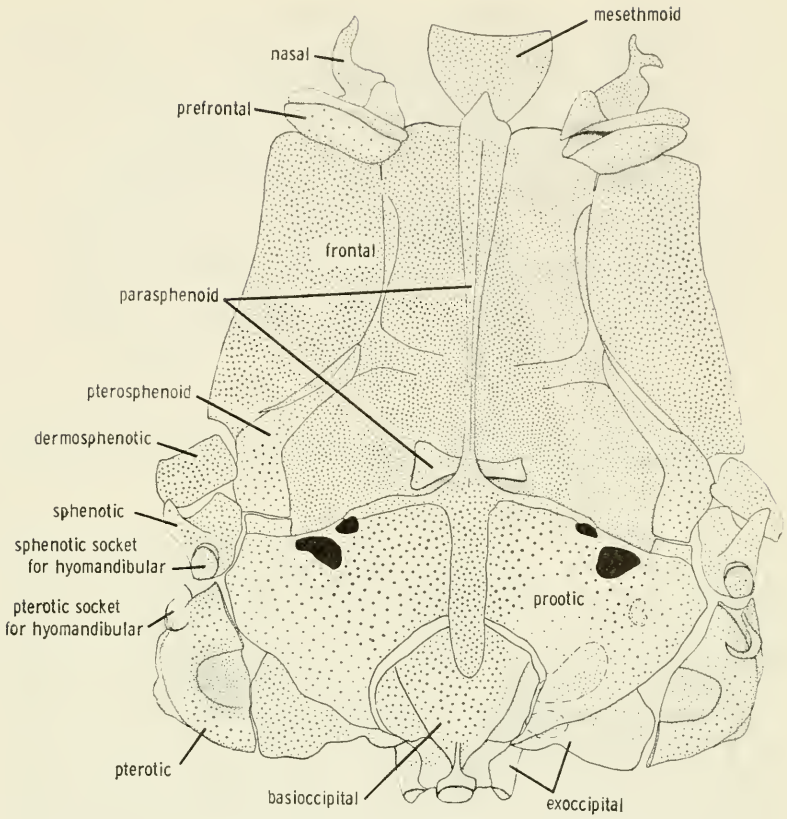

Fig. 4. Ventral view of cranium, 16.5-mm specimen.

only by lacrimal, preopercle and dermosphenotic bones. The very large eye is apparently unassociated with any radical modifications or displacements of bones. Subopercle very large, forming entire posterior margin of gill cover. Upper arm of subopercle terminating in a weak flange forming dorsal margin of an externally visible concavity in opercular margin just below dorsal origin of gill slit. Lower arm of subopercle with a strong, dorsally-directed flange lying between opercle and interopercle. Interopercle very elongate.

Jaws and jaw suspension (Figs. 6, 7). The jaws do not differ from what one would expect in a small, surface- or near-surface-feeding, insectivorous cyprinodont. Premaxillaries moderately pro-

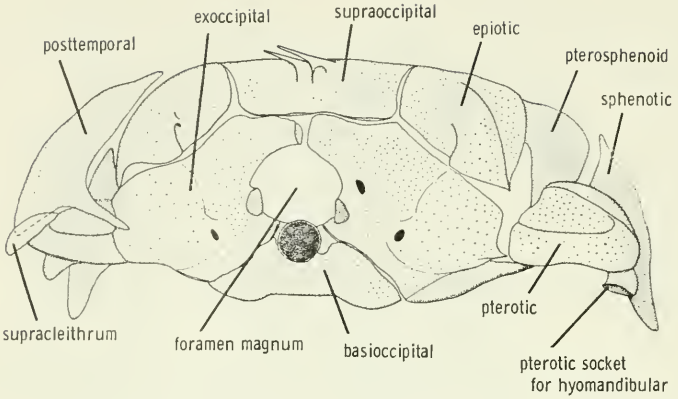

Fig. 5. Occipital view of cranium, 17.0-mm specimen. Pterosphenoid visible because frontal and dermosphenotic bones have been removed. Viewed from angle to right of fish.

tractile, ascending premaxillary processes broad-based and short, with rounded posterior margins. Maxillaries slender, with well-developed mesial and palatine processes. Mesial processes ligamentously attached to ventral surface of ascending premaxillary processes; back and forth movement of premaxillaries accompanied by equal movement of mesial maxillary processes, and when transmitted to distal portion of maxillaries (beyond palatine processes) these rotate on their axes while remaining in more or less the same vertical plane. An 11.5-mm specimen has about 26 teeth in upper jaw and 22 in lower; a 16.5-mm specimen, about 35-40 teeth in both jaws.

Hyomandibular bone with well-developed, separate joints for articulation of pterotic and sphenotic bones. Palatine, ectopterygoid, and entopterygoid intimately united (for discussion of these elements in cyprinodonts see Rosen, 1964: 232, fig. 10). Symplectic bone elongate. Quadrate with a slender, posteriorly-directed extension. Metapterygoid absent.

Hyoid and pharyngeal arches (Figs. 8, 9). The hyoid arch has the following peculiarities: 1) hypohyal of each side a single, undivided element; 2) interhyal absent; 3) branchiostegal rays, usually five on each side, articulating with ceratohyal; 4) urohyal with a strong, dorsally-directed process at its anterior end; and 5) epihyal and ceratohyal not rigidly joined by a dorsal bony ridge.

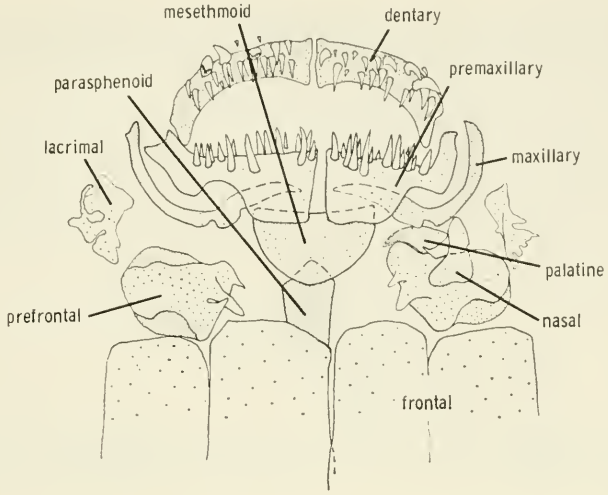

Fig. 6. Dorsal view of jaws and anterior bones of head, 16.5-mm specimen; head tilted back.

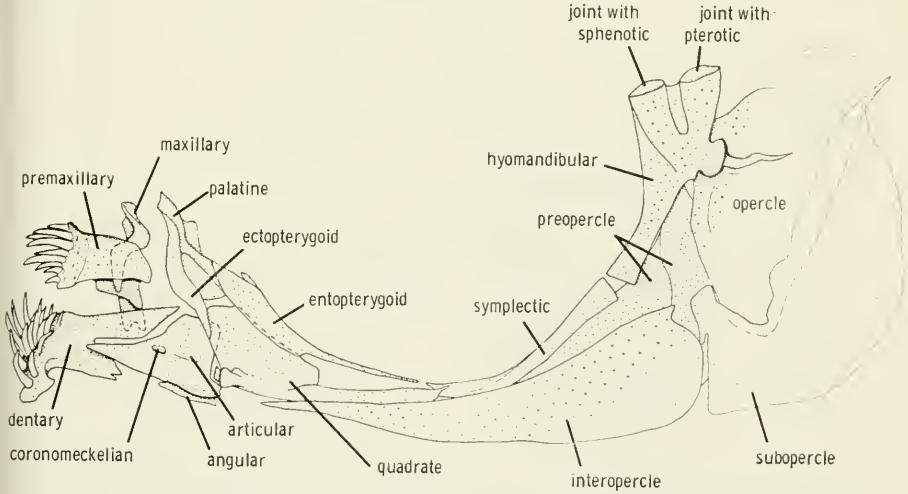

Fig. 7. Internal view of jaws, jaw suspension and opercular elements, 16.5-mm specimen.

Branchiostegal rays usually simple, but in 17.8-mm specimen anteriormost ray on one side with a hooklike, medially-directed process midway on its length.

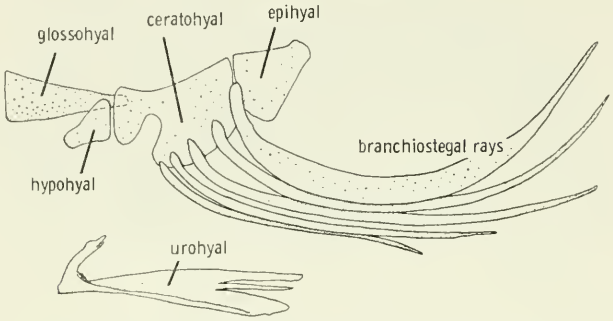

Fig. 8. External view of hyoid arch and urohyal (separated), 16.5-mm specimen.

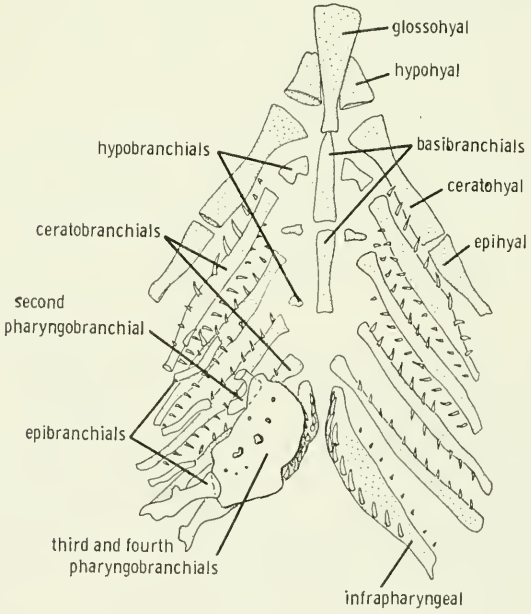

Fig. 9. Dorsal view of hyoid and pharyngeal arches, with dorsal elements shown on left side only, 16.5-mm specimen. Third hypobranchial on right side not ossified in this specimen; ossified in other specimens.

Pharyngeal arches with two elongate ossified basibranchials. First pharyngobranchial absent. Second pharyngobranchial intimately associated with but separate from upper pharyngeal plate, toothless in some specimens, in others bearing four to six conical teeth. Upper pharyngeals, presumably consisting of united third and fourth pharyngobranchials, with a dense patch of conical teeth. Lower pharyngeals of left and right sides not in contact, with two or three irregular rows of conical teeth.

Fig. 10. Frontal view of first vertebra, 16.5-mm specimen.

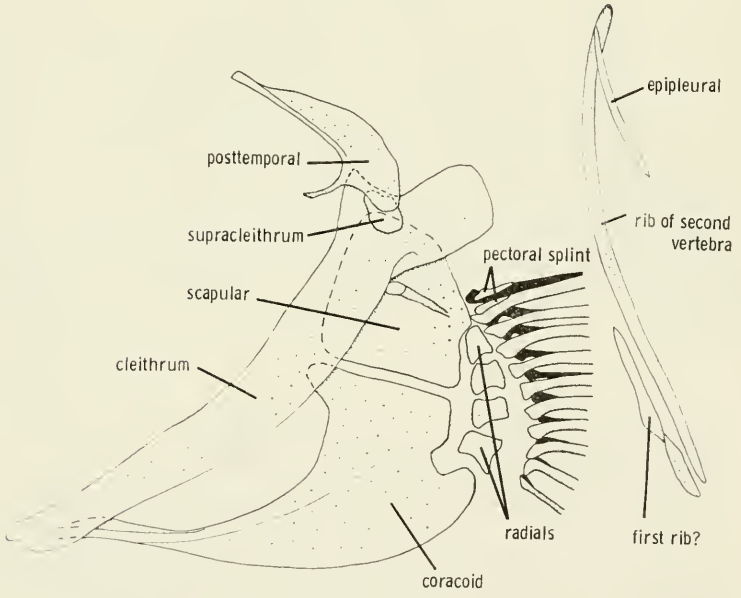

Fig. 11. External view of pectoral girdle, 16.5-mm specimen; first and second ribs drawn separately; in normal position they lie directly behind the radial bones, or behind radial bones and articulations with pectoral rays.

Vertebral column. Vertebrae 26 excluding hypural, 12 abdominal and 14 caudal or 13 abdominal and 13 caudal. First vertebra (Fig. 10) with complete neural arch, three condylar facets, and associated pair of epipleural intermuscular bones, without transverse processes or ribs. A small element associated with the distal end of the rib of the second vertebra is probably the true first rib (Fig. 11). This element is characteristic of cyprinodontoids; in *Oryzias melastigma* it is unusually long. Rosen and Bailey (1963: 31) interpreted what is evidently the same element in Poeciliidae as a secondary postcleithrum. In *Fluviphylax* it lies in the body wall, and is separated from the pectoral girdle by the deep pocket internal to the pectoral fin base. Remaining abdominal vertebrae with large, stout transverse processes to which are attached proximal tip of ribs, and simple epipleurals. In some specimens epipleurals fail to develop in association with posterior abdominal vertebrae. Caudal vertebrae lacking epipleurals. Haemal canals moderately large.

Pectoral girdle (Fig. 11). Posttemporal bone forked, upper limb articulating with epiotic, lower with exoccipital (intercalar absent). Supracleithrum small, scalelike, interposed between posttemporal and cleithrum. Scapular foramen present. Cleithrum rather slender. Lower limb of coracoid slender, its anterior end extending to near anteroventral tip of cleithrum; space between cleithrum and coracoid large. Postcleithra absent. Pectoral radials four. Pectoral splint present, consisting of two very short, bony splints tightly adherent to dorsal surface of ray halves of uppermost pectoral ray.

Pelvic girdle (Fig. 12). Distal tip of fifth rib ligamentously attached to dorsal surface of median pelvic projection. Posteriorly directed bony process of pelvic girdle very short, lacking in some specimens.

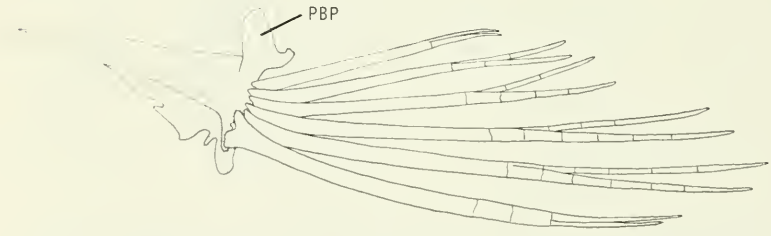

Fig. 12. Ventral view of left pelvic girdle and fin rays, 17.0-mm specimen. PBP = posteriorly directed bony process.

Caudal skeleton (Fig. 13). Hypural fan fused into a solid unit, even in 11.5—mm specimen, to which six of the eight principal caudal rays attach. Epural and haemal spines of hypural centrum each bearing a single principal ray.

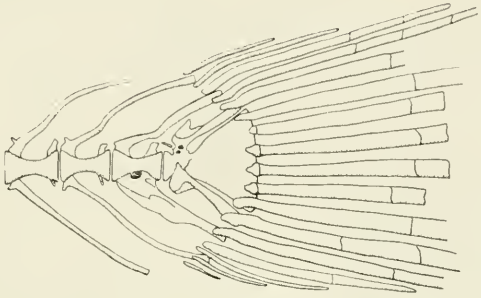

Fig. 13. Last three vertebrae and caudal skeleton, 11.5-mm specimen. Tiny separate element just above hypural centrum not evident in other specimens.

RELATIONSHIPS

The osteological characteristics of *Fluviphylax* are such that it does not fall automatically in any of the groups into which Sethi (1960) divided the oviparous cyprinodonts of the world (it is obviously unrelated to Pantanodontinae [Whitehead, 1962; Rosen, 1965] which Sethi did not consider), but they indicate that its relationships either lie with Procatopodinae or else with Fundulinae, and not with Rivulinae. In order to facilitate comparisons these characters of *Fluviphylax* are listed here (the order is similar to that employed by Sethi).

1. Mesethmoid a bony, double lamina.
2. Prevomer absent.
3. Nasal bones reduced.
4. Dermosphenotic prominent.
5. Parietals absent.
6. Anterolateral parasphenoid processes short, not contacting pterosphenoids.
7. Foramen magnum bordered exclusively by exoccipitals and basioccipital.
8. Exoccipital and basioccipital condyles well developed.
9. Transverse processes of first vertebra meeting dorsally, not articulating with occiput.
10. No distinct gap between first and second vertebrae.
11. Transverse processes of precaudal vertebrae stout and elongate.

12. Epiotic processes absent.
13. Metapterygoids absent.
14. Teeth strictly conical, disposed in two irregular rows on both jaws.
15. Premaxillary processes short and broad, extending over mesial maxillary processes.
16. Mesial maxillary processes large and ligamentously attached to ventral surface of ascending premaxillary processes.
17. Outer maxillary processes weakly developed.
18. Hypohyals consisting of a single element on each side.
19. Branchiostegal rays normally five on each side.
20. Third and fourth pharyngobranchials united.
21. Infrapharyngeals separated.
22. Two ossified basibranchials.
23. Posttemporal bone forked.
24. Supracleithrum present.
25. Postcleithra absent.
26. First rib greatly reduced, associated with distal tip of rib of second vertebra.
27. Large space between cleithrum and coracoid.
28. Posteriorly-directed, bony pelvic process short or lacking.
29. Haemal canals moderately large.
30. Hypural fan a solid piece.
31. Vertebrae 26.

Comparison with Rivulinae. Differences between *Fluviphylax* and Rivulinae are numerous and fundamental, the most important being that Rivulinae have a cartilaginous mesethmoid, toothed prevomer, metapterygoid, dorsal and ventral hypohyals on each side, separated third and fourth pharyngobranchials, and a hypural fan divided in two or even (in *Aplocheilus*) three parts. It should be noted that our knowledge of the osteology of *Rivulus* is based on a single species (*R. bondi* Schultz). Although there are many species of *Rivulus,* the genus is very constant in its characters (Myers, 1927: 119) and since Sethi found relatively few differences between *R. bondi* and other genera of Rivulinae it is reasonable to expect only relatively minor differences among various species of *Rivulus.* A number of non-osteological differences between *Rivulus* and *Fluviphylax* were pointed out above in the generic characterization of *Fluviphylax.*

Fluviphylax is a very distinct genus but is notably lacking in bizarre or "unexpected" specializations or distinctive osteological characters that would set it apart readily from all other cyprinodont groups. Most of its osteological characters occur in many or even in most cyprinodont groups, apart from Rivulinae, and thus are of little value in assessing phylogenetic relationships. Regarding character 31, 26 is near the lowest number of vertebrae in cyprinodonts.

Diminutive representatives of any group are likely to have reduced vertebral counts approaching this number. Since an overwhelming proportion of these characters occur in Procatopodinae and Fundulinae, in contrast to other groups, the relationships of *Fluviphylax* may lie with one of these two subfamilies.

Comparison with Procatopodinae. All Procatopodinae in which the osteology has been studied agree with *Fluviphylax* in characters 4-13, 17, 18, 20-22, 24, and 26-30, and one or more species also agree in characters 2, 14, 19, 23 and 25. In *Poropanchax rancureli* the prevomer is absent and the posttemporal is forked about as in *Fluviphylax* (personal observation). Perhaps the most important difference between Procatopodinae and *Fluviphylax* is that Procatopodinae have a cartilaginous mesethmoid and in none of the Procatopodinae is the mouth position quite as in *Fluviphylax*. On the other hand, the elevated pectoral fin position is virtually identical in *Fluviphylax* and Procatopodinae. In *Poropanchax rancureli* the three uppermost pectoral rays articulate with the scapula and the portions of the cleithra that form the posterior wall of the gill chambers are almost vertical, whereas in *Fluviphylax* only the uppermost pectoral ray articulates with the scapula and the posterior wall of the gill chambers is oblique. These observations suggest that the elevation of the pectorals in *Fluviphylax* and Procatopodinae may have been achieved in different ways. It should be noted that the pectoral fins are extremely elevated in the remarkable, tiny cyprinodontoid *Horaichthys,* presumably related to *Oryzias* (see Kulkarni, 1940: 379-423, and especially figs. 2 and 18). In *Horaichthys,* incidentally, the dorsal fin is very small and its position is more posterior than in any other cyprinodontoid. This suggests that the high-set pectorals, small, posteriorly-placed dorsals and reduced body size in many procatopodins and in *Fluviphylax* are functionally correlated characters.

Comparison with Fundulinae. All Fundulinae in which the osteology has been worked out agree with *Fluviphylax* in characters 1, 4, 7-11, 13, 15, 16, 18, 20-24, 26 and 28-30, and one or more species also agree in characters 6, 12, 14, 17, 19 and 25. The most important differences between Fundulinae and *Fluviphylax* appear to be that Fundulinae have a prevomer and parietals, and low-set pectoral fins with a restricted space between coracoid and cleithrum. Pectoral fin position and amount of space between coracoid and cleithrum may well be functionally correlated characters. The prevomer and probably the parietals have been lost in several cyprinodont lines, so their absence is not wholly unexpected in a

form so tiny as *Fluviphylax*. Most adult Fundulinae have posteriorly-directed epiotic processes but these develop late and are sometimes unformed in specimens the size of *Fluviphylax*. Of described Fundulinae, perhaps *Fundulus notatus* bears the greatest superficial resemblance to *Fluviphylax*. A fish derived from *F. notatus* but smaller (and with fewer vertebrae), with enlarged eyes, open instead of tubular cephalic laterosensory canals, a considerably shortened snout (involving loss of prevomer, reduction of nasal and lacrimal bones, and shortening of ascending premaxillary processes), slightly elevated pectoral fins (with an enlarged space between coracoid and cleithrum), and a more posteriorly placed dorsal fin (with fewer rays) would be exceedingly like *Fluviphylax*.

Whatever its relationships may be, *Fluviphylax* does not belong in any of the recognized subfamilies. Therefore a new subfamily is proposed for it.

FLUVIPHYLACINAE new subfamily

A subfamily of very small, oviparous cyprinodonts with exceptionally large eyes, free orbital rim, dorsal fin placed far posteriorly, pectoral fin set high, tips of pectoral fin rays extending beyond base of pelvic fins. The main osteological characters of the subfamily are listed and discussed above. The subfamily, perhaps ecologically equivalent to some of the African Procatopodinae, is known only from the Amazon basin.

DISCUSSION

Fluviphylax is closest phenetically to Procatopodinae, and perhaps it is also closest to them phyletically, but relationship with Fundulinae is too strong a possibility to be ignored. At least until the phyletic relationships of *Fluviphylax* are clearer it is best to recognize it as forming a monotypic subfamily, the Fluviphylacinae. In considering the relationships of *Fluviphylax*, I have refrained on purpose from zoogeographic speculation. In this instance zoogeographic aspects are so controversial they can only serve to confuse matters until relationships are clearly understood. That Procatopodinae are almost exclusively restricted to continental Africa is insufficient grounds to disqualify them as possible relatives of *Fluviphylax*. In this connection, I have tended to think of *Fluviphylax* as relatively recently derived simply because of its tiny size, a conclusion which may be quite erroneous.

Fluviphylax illustrates a feature of cyprinodont distribution that should be elaborated, namely that the tiniest forms occur in the midst of the world's richest fresh water fish fauna (Amazonas), whereas the relatively giant forms are found in situations geographically or ecologically isolated from rich fish faunas. The only other described oviparous cyprinodont (if it is truly an oviparous cyprinodont, and adult) as small as *Fluviphylax* is *Hubbsichthys laurae* Schultz, represented by a single 14-mm specimen from "Pampán, Estado de Trujillo, Venezuela, probably Río Motatán drainage" (Schultz, 1949: 96-97). The smallest viviparous cyprinodont, *Poecilia* (*Pamphorichthys*) *minor* (Garman), is Amazonian. As stated by Garman (1895: 92), "the length of the males is about seven-tenths of an inch and that of the females about eight" and "females of three-fourths of an inch in total length contain fully developed embryos." I have examined a 14.5-mm specimen collected by EPA in Lago Parauacui, near Oriximina, state of Pará, in which the gonopodium is fully mature and serrae are formed on the second ray in the pelvic fins of both sides (*cf.* Hubbs and Hubbs, 1945: 295-296, fig. 2). The types were obtained by the Thayer Expedition near Villa Bella, roughly a hundred miles up the main Amazon River from Obidos and about the same distance from Oriximina (for a map showing the route of the Thayer Expedition, as well as the routes of Spix and Martius, Castelnau, Natterer and Schomburgk, see Eigenmann, 1917, pl. 1).

Myers (1966: 769-771) pointed out that poeciliids apparently radiated into forms of diverse ecology and size in "the Ostariophysan vacuum" of Central America before Cichlidae arrived there. The advent of cichlids may have cut down this diversity, especially in the larger, stream-inhabiting poeciliids, "leaving the many smaller poeciliids, as in North and South America, only in what might be termed peripheral habitats." *Pamphorichthys* provides a beautiful example of a tiny poeciliid in a cichlid- and characid-rich environment.

Regarding the largest cyprinodonts, the Orestiidae occur only in Andean lakes and associated rivers and streams in Bolivia, Peru, and northern Chile at altitudes between eight and 16 thousand feet (Eigenmann and Allen, 1942). *Anableps, Belonesox,* and the largest species of *Fundulus* and of *Poecilia* all are brackish-water forms generally restricted to estuarine or near-estuarine habitats or are euryhaline and tend to occur either in fresh water where the fresh water fish fauna is relatively poor (e.g., *Belonesox*) or else in marine and semi-marine habitats where the marine fish fauna is

relatively poor (e.g., most of the largest species of *Fundulus*). I suspect that *Belonesox* would be unable to coexist with the predatory characoids *Hoplias* or *Ctenolucius,* and that this may have helped shape the southern boundaries of its range. Orestiidae may be unable to withstand the introduction of gamefish such as trout into their mountain retreats.

During fieldwork in Ghana I gained the impression that the largest Rivulinae there, particularly *Epiplatys,* usually occur in isolated situations such as in small streams above waterfalls or along the margins of swampy areas, where they are sometimes the only fishes present. I suspect that the largest Amazonian Rivulinae tend to be similarly isolated. The largest West African procatopodin, *Aplocheilichthys spilauchena,* generally is restricted to estuarine or near-estuarine habitats and the lowermost reaches of rivers. In a recent account of the Procatopodinae of Ghana, Scheel (1968: 277) did not mention the presence of this species there. It is abundant near the mouths of the Volta and Tano rivers and probably occurs in suitable habitats along the entire coast of Ghana. It is the only member of the Procatopodinae to occur on both sides of the Dahomey Gap, a fact explained by its essentially estuarine distribution. The species has been recorded from Senegal to lower Congo (Boulenger, 1915: 62), and from the island of Fernando Póo (Scheel, 1968: 278). It is apparently the only procatopodin to have reached a locality separated by the sea from continental Africa. It may have reached there in the not-too-distant past when the island probably was connected to the mainland, some sixty miles distant. The Procatopodinae, incidentally, may qualify as primary freshwater fishes, but we need more physio-ecological data to determine this.

Hoedeman (1956-61) worked out supposed homologies between scales in the dorsocephalic squamation in a large number of cyprinodont species and used this information as a basis for suggesting relationships at various taxonomic levels. Species and species-groups do have characteristic scale patterns, and these may be useful in determining relationships between forms in which the patterns have remained relatively unchanged. But the difficulties of interpretation increase proportionately as the number of scales changes or the patterns are radically different. The fundamental problem involves homologies. In two of the three major criteria for determining whether structures are homologous, morphology and embryology, the head scales presumably are all identical. That is, they have the same histological structure, and so far as we

know, arise from anlage which are indistinguishable one from another.

Hoedeman frequently explained reductions in number of head scales as being due to "fusions." Surely decreases and increases in the number of head scales correspond to the formation of fewer or more scale anlage, not to fusion or the analogous process implied, "splitting" of scales. Change in scale number probably is accompanied by partial or total rearrangement of spacing between scale anlage in an otherwise essentially uniform field with scale-forming potential. If this is so, is it not erroneous to apply homologies as Hoedeman has done?

The sole criterion Hoedeman used to determine homologies is that of relationships to other structures. He assumed that the scale overlying the pineal organ is homologous in all cyprinodonts (Hoedeman, 1958a: 23). He did not point out any anatomical connection between the pineal gland and this scale, however, and the relationship would seem to depend entirely on the superficial characteristic of position. Using this scale, the *"a scale,"* for a starting point, Hoedeman extrapolated the rest of his homologies according to the spatial relationships of the remaining scales to it and to each other. This is clearly a precarious operation. Granted that all cyprinodonts develop dorsocephalic squamation, one would expect to find a scale more or less directly over the pineal organ in every species. In fact, the exact position of the scale over the pineal organ varies considerably, and sometimes there are two scales side by side more or less directly above it. In Rivulinae, the scale in the "a" position usually is overlapped by all of the scales neighboring it, whereas in various species belonging to other subfamilies it is the topmost scale (Hoedeman, 1958a)!

On the other hand, some of the relationships between scales pointed out by Hoedeman are remarkably constant; furthermore, within groups the scales tend to remain in the same relationship to segments of the cephalic sensory canal system. In many cyprinodonts (*cf.* Rosen and Mendelson, 1960; Whitehead, 1962, fig. 12) what I would interpret as the *"g scale"* is unpaired and has a segment of the supraorbital cephalic sensory canal on either side of it; occasionally it is the anteriormost scale. Immediately behind it is a pair of *"e scales,"* which are frequently notched at their posterolateral borders where they are approached by the dorsalmost portion of the posterior infraorbital canal. Behind these *e scales* is a median scale (sometimes paired), the *a scale,* near the posterior margin of the eye. In cyprinodonts with such a pattern

perhaps we may speak in terms of homologies between scales in corresponding positions in different species.

As I have pointed out in another connection (Roberts, 1967: 251-252) reduction or loss of structures, which is to be expected in small species, frequently leads to convergent characters. In *Pantanodon podoxys* (Whitehead, 1962: 125-126, fig. 13), as in *Fluviphylax,* the dorsocephalic squamation is so reduced that it is of no help in assessing relationships. In the interpretation Whitehead hesitantly decided upon, *Pantanodon* has a large *h scale,* two *g scales,* two *e scales,* and a single *a scale.* According to this arrangement, not only is there a pair of *g scales,* but the *a scale* is further posterior than in any other cyprinodont! If homologies can be drawn between the scales in *Pantanodon* and other cyprinodonts, one might re-interpret Whitehead's two *e scales* as a pair of *a scales,* his pair of *g scales* as *e scales* (which are usually paired), and his *h scale* as a *g scale* (which is usually single). When this is done, it turns out that the dorsocephalic squamation in young *Pantanodon podoxys* is rather similar to that in *Fluviphylax.*

The remarkable silvery sheen on the dorsum of the eyes of *Fluviphylax* deserves further comment. A silvery sheen on the dorsal surface of the eyes is characteristic of certain African lampeyes (Procatopodinae) and also, surprisingly, of *Oryzias melastigma;* a similar color feature occurs in the little atherinoid *Pseudomugil signatus,* also known as the Australian Blue-eye (personal communication from N. R. Foster). An analogous silvery color, brilliantly visible when the fishes are viewed from above as they swim near the surface, is the shining occipital spot in *Aplocheilichthys spilauchena, Aplocheilus panchax, A. lineatus,* some species of *Epiplatys, Fundulus olivaceous, F. notti* (the Starhead topminnow), and *F. notatus* (personal communication from N. R. Foster and G. S. Myers). Miehe (1911) suggested that the occipital spot in *Aplocheilus panchax* facilitates capture of the insects it preys upon by luring them closer to the water surface. A more basic function may be to reflect harmful radiations so that they do not pass through the brain or eyes, as the case may be. In *Fluviphylax,* which generally inhabits shaded places, the eyes' silvery mantle may lessen the need for visual accommodation and minimize the dazzling effect of bright light as the fish swims into a sunlit area.

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(Received 28 January 1970.)

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THE RELATIONSHIPS OF THE SKINKS REFERRED TO THE GENUS *DASIA*

Allen E. Greer

ABSTRACT. The time honored lygosomine genus *Dasia* is divided into three genera (*Dasia*, *Lamprolepis* and *Apterygodon*) primarily on the basis of differences in skull osteology and external morphology. *Dasia* (6 species) and *Lamprolepis* (3 species) seem to have evolved independently from a primitive *Mabuya*-like ancestor, whereas *Apterygodon* (1 species) seems to have evolved from a basically *Dasia*-like stock. All three taxa appear to have had southeast Asia as their area of origin.

When Boulenger (1887) published his third volume of the Catalogue of the Lizards in the British Museum, he placed three species in the subgenus *Keneuxia*. In the two major revisions of lygosomine skinks since Boulenger (M. A. Smith, 1937; Mittleman, 1952), these three species plus other more recently described species have been grouped together in the genus *Dasia*. Yet in spite of the long historical precedent of treating these species as a generic entity, there are no characters that will serve to unite the species in a common genus, distinct from other skink genera. On the contrary, there are several characters by which the species can be assigned to three distinct genera, *viz.*: *Dasia* (6 species), *Apterygodon* (1 species), and *Lamprolepis* (3 species).[1] Curiously enough, the type species of the three genera are the three species that comprised Boulenger's (1887) subgenus *Keneuxia*.

In Table 1 I have listed, roughly in order of what seems to me to be their taxonomic importance, the characters that readily serve to distinguish the three genera.

[1] The names of the two genera beside *Dasia* are available from the primary synonymy of *Dasia*.

TABLE 1

A summary of the diagnostic characters of the three genera of skinks previously grouped together in the genus *Dasia*.

Dasia (6 species)	*Apterygodon* (1 species)	*Lamprolepis* (3 species)
Palatal rami of pterygoids meet medially (Fig. 1).	Palatal rami of pterygoids meet medially (Fig. 3).	Palatal rami of pterygoids separated medially; medial processes from palatines project posteriorly into interpterygoid vacuity (Fig. 1).
Pterygoid teeth present (Fig. 1).	Pterygoid teeth absent (Fig. 3).	Pterygoid teeth absent (Fig. 1).
No ectopterygoid process to palatine; palatal ramus of pterygoid borders infraorbital vacuity (Fig. 1).	Ectopterygoid process to palatine excludes much of palatal ramus of pterygoid from a position on the infraorbital vacuity (Fig. 3).	No ectopterygoid process to palatine; palatal ramus of pterygoid borders infraorbital vacuity (Fig. 1).
Young with sharply delineated light and dark crossbands which may or may not persist into adulthood (Fig. 2).	Adults with five white stripes on the very dark anterior part of the body; no crossbands. Young unknown.	Young and adults more or less uniformly colored and patterned. Any patterning tends to run longitudinally; no cross bars or stripes at any stage in life.
Gait slow.	Gait not slow.	Gait not slow.
Keeled body scales.	Keeled body scales.	Smooth body scales.
Postorbital bone present or absent.	Postorbital bone present.	Postorbital bone absent.
A pair of nuchal scales.	No, or rarely 1, pair of nuchal scales.	One or more pairs of nuchal scales.
Interparietal completely separates parietals except in some *haliana*.	Interparietal completely separates parietals.	Parietals meet behind interparietal.

Dasia Gray

Dasia Gray, 1839, Ann. Mag. Nat. Hist., vol. 2, p. 335 (Type species: *Dasia olivacea* Gray, 1839, by monotypy).

Liotropis Fitzinger, 1843, Systema Reptilium, p. 22 (Type species: *Euprepes ernestii* Duméril and Bibron, 1839 = *Dasia olivacea* Gray, 1839, by monotypy).

Theconyx Annandale, 1906, Spolia Zeylanica, vol. 3, p. 191 (Type species: *Euprepes halianus* Haly and Nevill, 1887, by monotypy; not *Theconyx* Gray, 1845).

Diagnosis. Of all the skinks with supranasal scales (*Apterygodon, Dasia, Emoia, Eugongylus, Eumecia, Lamprolepis, Mabuya, Macroscincus, "Otosaurus,"* and *Riopa*) only *Dasia, Eumecia, Mabuya* (17 of 30 species examined), and *Riopa* (3[1]of 13 species examined) have pterygoid teeth. *Eumecia* is a genus encompassing one or two species with greatly reduced appendages and digits and is easily distinguishable from the strong-limbed, pentadactyl *Dasia. Dasia* differs from *Riopa* and *Mabuya* in palatal characters: in *Dasia* the palatal rami of the pterygoids meet medially, whereas they are separated by an interpterygoid vacuity in *Mabuya* and by posteriorly projecting medial processes from the palatines in *Riopa* (Fig. 1).

Referred species. Griffini Taylor, 1915; *haliana* Haly and Nevill, 1887; *moultoni* Barbour and Noble, 1916; *olivacea* Gray, 1839; *semicincta* Peters, 1867; *subcaerulea* Boulenger, 1891.

There may be more species of *Dasia* than those listed here, for Taylor (1963) believes that "more than a single species" has been confused under the name *olivacea.*

Distribution. Extreme southwestern India (*subcaerulea*); Ceylon (*haliana*); southern Thailand, Cambodia, Laos and Vietnam south of 15° N Lat., Con Son, the Andaman and Nicobar Islands, Borneo and Java (*olivacea*); Palawan Islands (*griffini*); Philippines (*semicincta*). *Moultoni* occurs on Borneo with *olivacea* in the only known case of sympatry between any two species in the genus. The distribution is disjunct; there are no species between southern India and Ceylon and southeast Asia.[2]

[1] In an earlier paper (Greer, 1967b) I said that only 1 (*bowringi*) of these 13 species had pterygoid teeth. This is not correct, for a re-examination of this material shows two additional species (*afer* and *punctata*) with pterygoid teeth.

[2] This particular disjunct distribution is relatively well known in other reptiles and vertebrates. See the symposium on the zoogeography of this distribution in the Proc. Nat. Inst. Sci. India, vol. 15, no. 8, 1949.

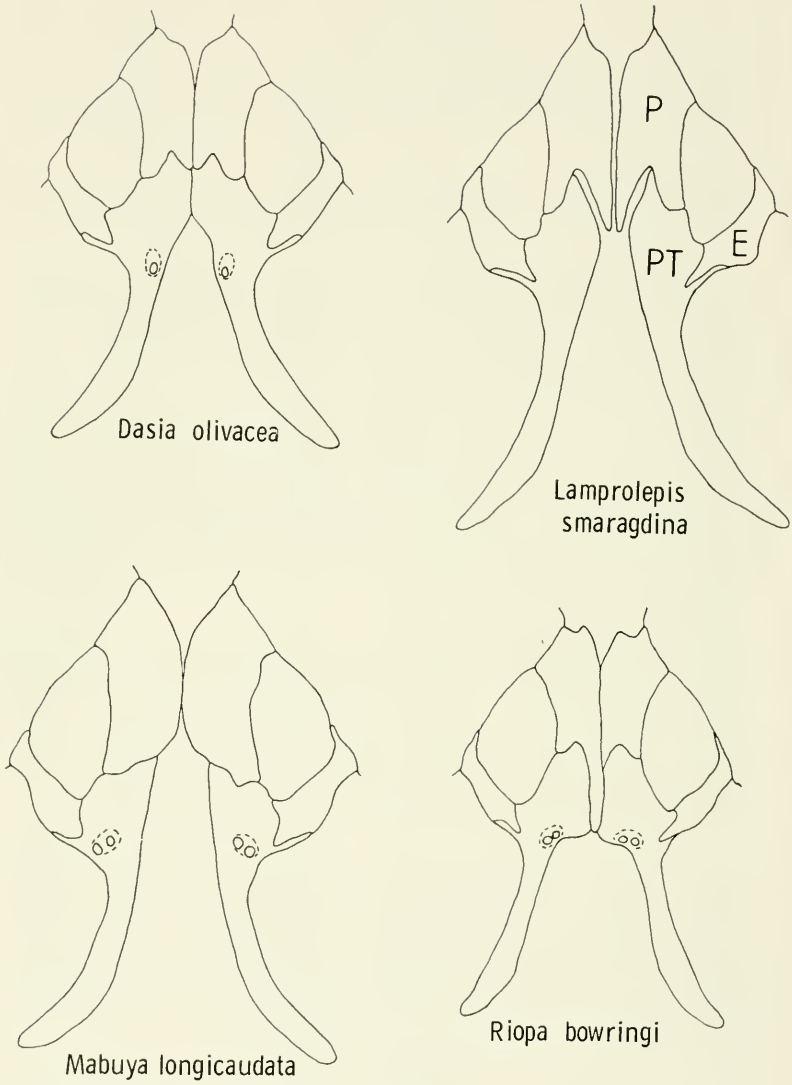

FIGURE 1. Ventral view of the secondary palate in *Mabuya longicaudata*, a primitive lygosomine, and representatives of three genera—*Dasia*, *Lamprolepis* and *Riopa*—thought to have evolved independently from an ancestor much like this primitive lygosomine. Not drawn to scale. Abbreviations: E, ectopterygoid; P, palatine; PT, pterygoid.

Although it is evident from the distribution outlined above, I should perhaps emphasize that *Dasia*, although quite widespread in southeast Asia and the western end of the Indo-Australian Archipelago, is an almost classic example of a taxon whose easternmost distributional limits extend to, and thereby help to define, Wallace's Line.

Species taxonomy. Several factors make it difficult to know where the species boundaries should be drawn in this genus. First, with the exception of *moultoni* and *olivacea* on Borneo, all the species are allopatric. Second, with the exception of the Ceylonese *haliana*, the species are very similar in several classically important scale counts, and third, two of the species (*moultoni* and *subcaerulea*) are only known from single specimens. In view of these difficulties it may be worthwhile for me to express my opinions of the species taxonomy of *Dasia*.

Taylor (1922) proposed that *griffini* (Palawan) and *semicincta* (Philippines) be reduced to the rank of subspecies of the widespread *olivacea* of southeast Asia. Although the three forms are similar in several important scale counts, the following features serve to separate them and, to me, suggest specific status for each.

olivacea	*griffini*	*semicincta*
Supranasals separated	Supranasals meet	Supranasals meet
Black bands broader than light bands in young	Black bands about equal to light bands in young	Black bands broader than light bands in young (Fig. 2)
Postorbital bone present	?	Postorbital bone absent

I have been able to examine only a single skull of two of the species, but as I have never found the presence or absence of the postorbital to vary intraspecifically in skinks, I do not hesitate to accept it as a reflection of specific difference until more material is available to prove otherwise. Unfortunately I have not been able to see a skull of *griffini*.

The type and only known specimen of *moultoni* is a young individual that differs from the only other *Dasia* occurring with it on Borneo, i.e., *olivacea*, in having the supranasals meeting medially instead of being separated and in having the black bands narrower, instead of broader, than the light bands. *Moultoni* is most similar to *griffini* on Palawan, which has the black bands equal in width

to the light bands and which shows, as a variation, 3 of the 4 supraoculars in contact with the frontal, as is the case in the type of *moultoni*. Other *Dasia* and some *griffini* have but 2 of the 4 supraoculars in contact with the frontal.

Only two specimens of the south Indian *subcaerulea* are known, and the similarity between this species and the southeast Asian *olivacea* is reputed to be remarkable (M. A. Smith, 1935, 1949). Apparently the most noticeable difference between the two species is the presence of two black streaks on the neck of *subcaerulea* that are never present in *olivacea*. The great geographic distance between the two species is no assurance that other, as yet undiscovered, difference might exist between the two species, for as mentioned above (see footnote on page 3), the relationships between many vertebrates in the two separate areas of southern India-Ceylon and southeast Asia are surprisingly close. There are, however, only a few examples of conspecific relationship between nonflying animals in the two areas, and this fact, along with the slight differences that do exist between the two forms, tend to make me retain *subcaerulea* and *olivacea* as distinct species.

The Ceylonese *haliana* is readily distinguished from other *Dasia* on the basis of a lower number of longitudinal scale rows at midbody (24 instead of 26-30) and in the persistence of the juvenile banding into adulthood.

Reproduction. Information on the mode of reproduction is available for only two of the six species of *Dasia* and both are oviparous. M. A. Smith (1935) says that *olivacea* is oviparous and lays "six eggs at a time," but Cantor (1847) found 11 eggs in one female. Deraniyagala (1953) reports that a captive *haliana* laid "two soft-shelled eggs."

Field notes. As far as is known all the species of *Dasia* are arboreal to semiarboreal.

According to M. A. Smith (1935) and Taylor (1922), *olivacea* is arboreal and subarboreal in its habits and, in addition, shows "a preference for small islands" (M. A. Smith, 1935). Hendrickson (1966) found that on Palau Tioman, *olivacea* occurred mainly on the coastal plain where it replaced the upland *Mabuya multifasciata*, but it was not as common in its lowland habitat as was *M. multifasciata* in the upland forest.

Mr. James P. Bacon, Jr., who has observed *olivacea* from platforms in the forests of Sarawak, informs me (letter of 15 July 1968) that he and his group saw ten specimens, all of which were above 50 feet from the forest floor, and with respect to sites and

types of activity were similar to *Apterygodon vittatus* (see below). There was, however, one major difference between these two arboreal skinks: "In comparison to *vittatus,* which scampers around like a terrestrial *Mabuya* or *Sphenomorphus, olivacea* moves with almost painful deliberateness."

Taylor (1915, 1922) has the following comments on *Dasia semicincta,* a close relative of *olivacea:* "Specimens of this species were collected from the tops of large felled trees. It is a retiring species and is never observed on the ground," and "it is retiring and is seldom observed. It is arboreal in habit, feeding for the most part in the trees. Usually the animals inhabit trees which are densely covered with vines."

W. C. Brown (letter of 20 June 1968) has very kindly summarized for me his observations on *Dasia griffini,* a close relative of both *olivacea* and *semicincta:* "The specimens of *griffini* were collected in dipterocarp forest between 200 and 1000 feet elevation in the Thumb Peak area of Palawan. Most were taken in bark crevices or beneath loose bark on both living and dead trees. Two [were] collected on rocks on the river bank. . . . This is not an abundant species."

All we know of the ecology of *subcaerulea* is that the type and second known specimen were collected at 1100 and 5900 feet altitude respectively. M. A. Smith (1949) thought that the subdigital lamellae of the species indicated that it had "arboreal habits."

Dasia haliana is considered by Deraniyagala (1953) to be a "rare arboreal species restricted to the low country" of Ceylon. The same author mentions two individuals being captured from a hole and a cavity of a tree, respectively, and "according to Haly it lives on the tops of high trees" (Smith, 1935).

Deraniyagala (1953) provides another important clue to the behavior of *haliana* in his comment, "the gait of this arboreal species is much slower than in other Ceylon skinks even when climbing a tree." This comment calls to mind Bacon's statement of the "almost painful deliberateness" with which *olivacea* moves about the trees. One wonders if the slow movements of these two species may not be characteristic of all the species of *Dasia* in contrast to the more usual, quicker motions of the species of the other two genera recognized here.

Juvenile color patterns. As far as is known, all juvenile *Dasia* are strikingly marked with light and dark crossbands. The bands persist in adult *haliana* but disappear with age in the other species for which information is available.

Taylor's (1922) account of a juvenile *semicincta* is the most vivid available for any species in the genus: "The body above is glossy coal black with a series of brilliant orange yellow bars from the tip of the snout to the end of the tail. . . . The legs and digits [are] barred with canary yellow; the regenerated tail is brick red; below, on [the] body the bars widen and lose themselves in the immaculate canary yellow of the abdomen." There is a total of eight to nine yellow bars on the neck and body of this specimen described by Taylor. Another juvenile with ten light crossbands on the neck and body is shown in Figure 2.

FIGURE 2. Dorsal view of a juvenile (snout-vent length = 57 mm) and adult (snout-vent length = 117 mm) *Dasia semicincta* from the Philippine Islands showing the light and dark crossbands in the juvenile and their absence in the adult.

According to M. A. Smith (1935), "young [*olivacea*] are black above, with narrow silvery or yellowish, rather irregular transverse crossbars, from 11 to 14 in number, on the neck and body."

A late juvenile or subadult *griffini* (snout-vent length = 67 mm) in the Museum of Comparative Zoology (MCZ) may indicate something of the juvenile coloration for this species. This specimen is light brownish above with 14 dark brown crossbars, encompassing 13 light interspaces, from the nape to the base of the tail.

The type and only known specimen of *moultoni* is in the MCZ. It is clearly a juvenile (snout-vent length = 45 mm) and is predominately yellowish brown with 14 narrow dark brown crossbands, separated by 13 wider light interspaces, from the nape to the base of the tail. The crossbands extend laterally to, but not across, the venter.

In *haliana* "the number of black crossbands [in both juveniles and adults] varies from five to six from the shoulders to above [the] hips. . . . The width of the black bands alters with age. In the young they are equal to or only slightly narrower than the light interspaces. . . ." (Deraniyagala, 1953). Annandale (1906) figures a juvenile *haliana* in which there are seven dark crossbands, encompassing six light interspaces, from the nape to the base of the tail. According to Deraniyagala (1953) the "young [are] pink with black crossbands."

The two known specimens of *subcaerulea* are 57 and 70 mm in snout-vent length, but both lack any trace of crossbarring. It would seem, therefore, that either this species has no crossbanded pattern in the juvenile or the only known specimens are too old to display them.

The most interesting question about these crossbanded patterns is, of course, their function. Their function, however, is almost surely related to the ecology and behavior of their bearer, and as we know precious little of these matters in the adults and nothing in juveniles, we have very few facts with which to work.

Striking crossbanded patterns such as those seen in *Dasia* are really quite unusual in skinks, whether adult or juvenile. In fact, there are only about six other species among the approximately 800+ species of skinks that have an even closely comparable pattern, *viz.*: the scincines *Scincopus fasciatus, Scincus scincus* (some individuals), and *Scelotes splendidus*, and the lygosomines *Sphenomorphus fasciolatus, Tiliqua occipitalis* (some individuals), and *T. gerrardi* (especially pronounced in juveniles).

Other morphological evidence argues against a common ancestry for *Dasia* and any of these other species with crossbanded patterns, so their similarity in this regard is truly convergent.

The species of this list do share one ecological similarity, i.e., they are all ground dwellers that occasionally penetrate the loose substrate, but this is not a particularly unique ecological situation for skinks and it carries no ready explanation of the adaptiveness of the crossbanded pattern in such a situation.

Perhaps the juvenile color patterns are mimetic, taking advantage of either a specific but as yet unknown aposematic model or a general abstract model recognizable to predators gaining their experience with several different specific models. It could also be that the young occupy the same general habitat as the parents, and the juvenile color pattern acts as a signal to inhibit feeding attacks by the adult.

Relationships with other genera. In any group of skinks it is reasonable to assume that pterygoid teeth and supranasal scales are primitive features which may be lost in more advanced species. In possessing these two characters, therefore, *Dasia* is a primitive genus. On the basis of the secondary palate, however, *Dasia* is advanced, for the close medial apposition of the palatal rami of the pterygoids may be reasonably thought of as the extreme development of the uniquely scincid secondary palate (Greer, 1970).

The only living lygosomines that are like *Dasia* in retaining both supranasals and pterygoid teeth are *Riopa, Mabuya,* and *Eumecia.* Of these three genera, *Mabuya* is the best candidate for the closest ancestral relative of *Dasia.*

Eumecia is an African genus with one or two species. The taxon is very similar to *Mabuya* in its skull morphology and is distinguishable from this genus solely by its attenuate body form and reduced appendages and digits. *Eumecia* is clearly derived from *Mabuya* (Greer, 1967b), and its diagnostic specializations make it an unlikely ancestor for any other living skink.

If one combines all the primitive features of the various species of *Riopa* (exclusive of *Eugongylus*), the similarities with *Dasia* are impressive; supranasal scales, scaly lower eyelid, pterygoid teeth and oviparity. There is, however, an important difference in the relationships of the bones of the secondary palate, for in *Riopa* the pterygoids are separated by close-fitting, posteriorly-projecting medial processes from the palatines (Fig. 1), whereas in *Dasia* the

pterygoids meet medially and are not separated by palatine processes. In both genera the secondary palate, initiated by the medial apposition of the palatine bones, is extended further posteriorly by the partial (*Riopa*) or complete (*Dasia*) incorporation of the pterygoids. A posterior extension of the secondary palate is undoubtedly an advanced condition in lygosomines, but there is only a functional similarity between *Riopa* and *Dasia* in this regard, for the way in which the complete secondary palate is extended posteriorly, is fundamentally different in both taxa.

In addition to the palatal differences between *Riopa* and *Dasia* which preclude any close phylogenetic relationship, there are other important differences between the two groups. *Riopa,* for instance, lacks the crossbanded patterns in the young that are characteristic of *Dasia,* and it is also an essentially terrestrial taxon in contrast to the arboreal *Dasia.*

Mabuya is quite unlike both *Dasia* and *Riopa* in that the palatal rami of the pterygoids are widely separated with their medial edges smoothly diverging posteriorly (Fig. 1). This palate is primitive for lygosomines in the sense that the pterygoids are in an "uncommitted" state and could theoretically be incorporated into the secondary palate in a number of ways. In fact, it is this primitive palatal condition, along with the presence of supranasal scales, scaly eyelids, pterygoid teeth, well-developed pentadactyl limbs, a full complement of distinct head scales, and oviparity that makes *Mabuya* (especially the southeast Asian species in which all these characters occur) a very likely candidate for the ultimate ancestor of any lygosomine skink. In this light, it is easy to regard *Dasia* as being derived from a primitive *Mabuya*-like ancestor by the medial apposition and ultimate meeting of the palatal rami of the pterygoids along the midline.[1]

Dasia is similar to *Mabuya* in regards other than the sharing of the primitive lygosomine characters mentioned above. The body scales of *Dasia* (primarily the posterior body scales in adults) are keeled, as are the body scales of all the species of *Mabuya* except those eight or nine species (exclusive of *M. atlantica*) inhabiting the New World; these have smooth scales. Also, unlike *Riopa* and *Eumecia,* which are largely terrestrial and cryptic in their habits,

[1] Similarly, one can conceive of the evolution of *Riopa* from a primitive *Mabuya* through the medial apposition of the palatal rami of the pterygoids concurrently with the posterior extension of medial palatine processes (Fig. 1).

many species of *Mabuya* are partly arboreal in their habits. Such a propensity for arboreality could have provided the behavioral background on which to build the morphological adaptations to arboreality in *Dasia*.

To summarize this section we may outline the changes that occurred in the evolution of *Dasia* from a primitive *Mabuya*-like ancestor (also see Fig. 6).

1. The apposition of the palatal rami of the pterygoids along the midline of the secondary palate until they met and formed a posterior extension to the secondary palate.
2. The evolution of a striking crossbanded pattern in the young.
3. The evolution of a greater degree of arboreality.
4. The development of a slower gait.

Zoogeography. It is interesting to note that *Dasia* occupies the same general southeast Asian area occupied by the species that seem to be its closest ancestral relatives, i.e., the primitive species of *Mabuya*. In fact, like *Dasia*, *Mabuya* is, with only one or two exceptions, also confined to the area west of Wallace's Line. It looks, therefore, as if the evolution of *Dasia* from a *Mabuya*-like ancestor, and perhaps even the early evolution of *Mabuya* itself, is a phenomenon of the tropical parts of the southeastern Oriental Region and has had little or nothing to do with the area east of Wallace's Line, i.e., Wallacea and the Australian Region.

Apterygodon Edeling

Apterygodon Edeling, 1864, Nedel. Tijdschr. Dierk., vol. 2, p. 201 (Type species: *Apterygodon vittatum* Edeling, 1864, by monotypy).

Diagnosis. Along with *Dasia*, *Apterygodon* differs from all other skinks with supranasal scales in having the palatal rami of the pterygoids meeting medially along the midline of the palate. *Apterygodon*, however, differs from *Dasia* in lacking pterygoid teeth and in having a small fingerlike process of the ectopterygoid bone that projects anteriorly toward the palatine and partially excludes the palatal ramus of the pterygoid from a position on the infraorbital vacuity (Fig. 3).

Referred species. Only the type species is placed in the genus.

Distribution. Borneo. There is also a single specimen in the British Museum (Natural History) which is questionably from Ceram. This locality is almost certainly in error, however, for, with the exception of the Ceram record, the species has never been recorded from anywhere other than Borneo.

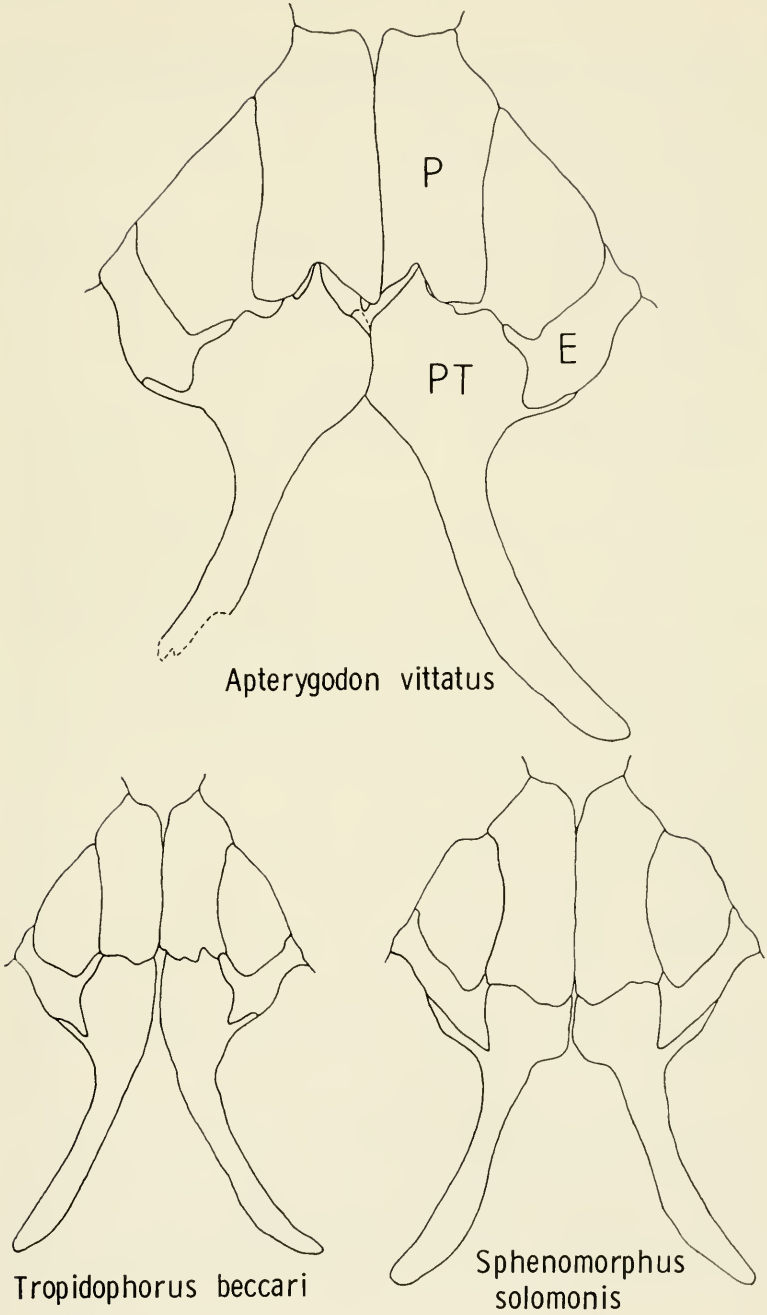

FIGURE 3. Ventral view of the secondary palate in *Apterygodon* and representatives of two other genera, *Sphenomorphus* and *Tropidophorus*, with species displaying similar palates. The ectopterygoid process has probably evolved independently in each of these three groups. The palatal bones of *Apterygodon* are partially disarticulated. Not drawn to scale. Abbreviations as in Figure 1.

Mode of reproduction. A female with a snout-vent length of 71 mm, collected in the Baram District of Sarawak, contains two eggs in the right oviduct and one in the left oviduct. The three eggs are surrounded by a fairly thick shell which indicates that the species is probably oviparous.

Field notes. By letter, Mr. James P. Bacon, Jr. has very generously summarized for me his observations on *vittatus* which were made in the course of platform observations on the altitudinal stratification of the reptiles in the Sarawak forest. Below, I have paraphrased the information on this species contained in Mr. Bacon's letter of 15 July 1968.

In one year of platform work from 36 to 110 feet above the forest floor there were 169 observations of *vittatus.* On the basis of number of observations, *vittatus* was the most frequently encountered lizard; a *Draco* was the second most frequently encountered species with 32 observations. *Vittatus* occurs between 0–120+ feet. The majority of the observations were made between 40 and 120 feet, although this range may reflect platform distribution more than it does lizard distribution. The observations made so far indicate that *vittatus* is the dominant canopy lizard in Sarawak, at least in the upper canopy (A and B strata).

Vittatus is a sunloving skink and moves about on trunks and branches of all kinds during the day. It spends its time exploring bark crevices and the interiors of epiphytes and in basking. The lizards are capable of short (half a foot or less) jumps between adjacent branches and vines.

Dr. Robert Inger has also given me his brief but valuable impressions about *vittatus* in the field. He says in a letter of 28 June 1968 that "*vittatus* is a sun lover. On rare occasions *vittatus* will descend to the ground, but only at the base of large trees."

Variation. Undoubtedly because of its canopy-dwelling habits (see "Field notes" section for the genus), *Apterygodon vittatus* is a little known skink. The Museum of Comparative Zoology is fortunate in having 15 specimens, and it is worthwhile to record the variation in several taxonomically useful characters for these specimens. All the specimens are from Sarawak.

The prefrontal scales are separated in all specimens, but two individuals have the scales of the snout broken up into a number of small, asymmetrical scales. Nuchal scales are lacking except in two individuals, which each have a single pair. There are always 4 supraoculars with 2 (in 18 of the 30 possible cases) or 3 (in the remaining 12 cases) supraoculars in contact with the

frontal. The fifth supraocular is beneath the eye except in one of the 30 possible cases where it is the fourth. There are 28-30 longitudinal scale rows at midbody, and 16-22 (avg. = 18.2) subdigital lamellae beneath the fourth toe. All 15 specimens are adults, and the largest two are each 72 mm in snout-vent length.

Relationships with other genera. Except for the absence of pterygoid teeth and the presence of an ectopterygoid process, *Apterygodon* and *Dasia* are very similar in several important skull characters. In both taxa there is a small postorbital bone, the palatal rami of the pterygoids are similar in shape in both taxa and meet medially, and there are 9 teeth on the premaxillae. The skull differences between the two genera do not really preclude the idea of the close relationship, for, as will be shown below, an ectopterygoid process has probably evolved numerous times in lygosomines, and the loss of pterygoid teeth is a familiar feature of lygosomine evolution.

Two aspects of the external morphology of the two genera make the idea of their close relationships even more compelling. The more remarkable of these is the numerous fine, approximately longitudinal striations on the dorsal and lateral body scales and the scales of the appendages. These striations were first noted by M. A. Smith (1935) in *Mabuya longicaudata* and were later rediscovered by Taylor and Elbel (1958) in *Dasia olivacea* and *Mabuya longicaudata.* An extensive examination of other lygosomines has revealed the striations only in *Dasia semicincta, D. griffini, D. moultoni* (the only species of *Dasia* available for examination), *Apterygodon,* and *Mabuya tytleri.* The striations, therefore, seem to be confined to *Dasia, Apterygodon,* and two species of southeast Asian *Mabuya,* i.e., those *Mabuya* which are most similar to the probable ancestor of *Dasia.* It appears then that the striations are another indication of the close relationships within this group of skinks. Unfortunately, the function of these striations is completely unknown.

The second external character that aligns *Dasia* and *Apterygodon* is a pair of enlarged "heel scales" on the rear foot in the males of both taxa. These scales in males are not only considerably larger than the surrounding scales, but they also seem to have an inner texture (viewed through the semitransparent epidermis) which distinguishes them from nearby scales and which belies a glandular function. In females this pair of scales is only slightly larger than the surrounding scales, and they appear to lack the textural differences that distinguish the scales from their fellows in

males. Paired enlarged heel scales are also evident in some *Mabuya,* but only in a few species (most notably *M. longicaudata*) are they larger (and then only slightly) in males than in females, and they are never differentiated as in male *Dasia* and *Apterygodon* (Fig. 4). The heel scales of *Mabuya* are probably homologous with those of *Dasia* and *Apterygodon,* but only in this latter group have they become greatly differentiated (to serve a glandular function?) in males.

Because we know nothing about the juvenile color patterns of *Apterygodon,* we have no idea how the genus compares with *Dasia* in this important regard. It seems unlikely, however, that a skink with an adult color pattern of anterior light longitudinal stripes on a dark ground color would have a juvenile color pattern consisting of light and dark crossbands, but admittedly my feeling on this may stem more from a sense of "taste" than from biological logic.

Aside from the differences in adult and possibly juvenile color pattern, the only other nonskeletal difference of any significance between *Apterygodon* and *Dasia* is in the gait, for, as mentioned above (see "Field notes" section under *Dasia*), *Apterygodon* has a faster, more commonly "skink-like" gait than does *Dasia.*

In summary, the differences between the two taxa are important but do not override the similarities on which the idea of their close relationship rests. I think, however, the differences do serve to justify the generic separation of the two taxa. In attempting to interpret these similarities and differences phylogenetically, we can hypothesize that *Apterygodon* and *Dasia* once shared a common ancestor that was decidedly *Dasia*-like except for the slower gait (and cross-banded juvenile color pattern?), and from this ancestor, *Apterygodon* evolved on the one hand through the loss of the pterygoid teeth and the independent evolution of an ectopterygoid process, and *Dasia* evolved on the other hand through a line that subsequently acquired a slower gait (Fig. 6).

Since this view of the phylogeny of *Apterygodon* and *Dasia* implies that the ectopterygoid process in *Apterygodon* has evolved independently of its evolution in other lygosomines, perhaps a word should be said about the significance of this process in lygosomines in general. It is true that the process, especially when it is well developed to the point of forming a firm articulation with the palatine bone, correlates well with other characters, which, taken together, serve to delimit large natural groups (Greer, 1967a). That this process, however, is not indicative of one and

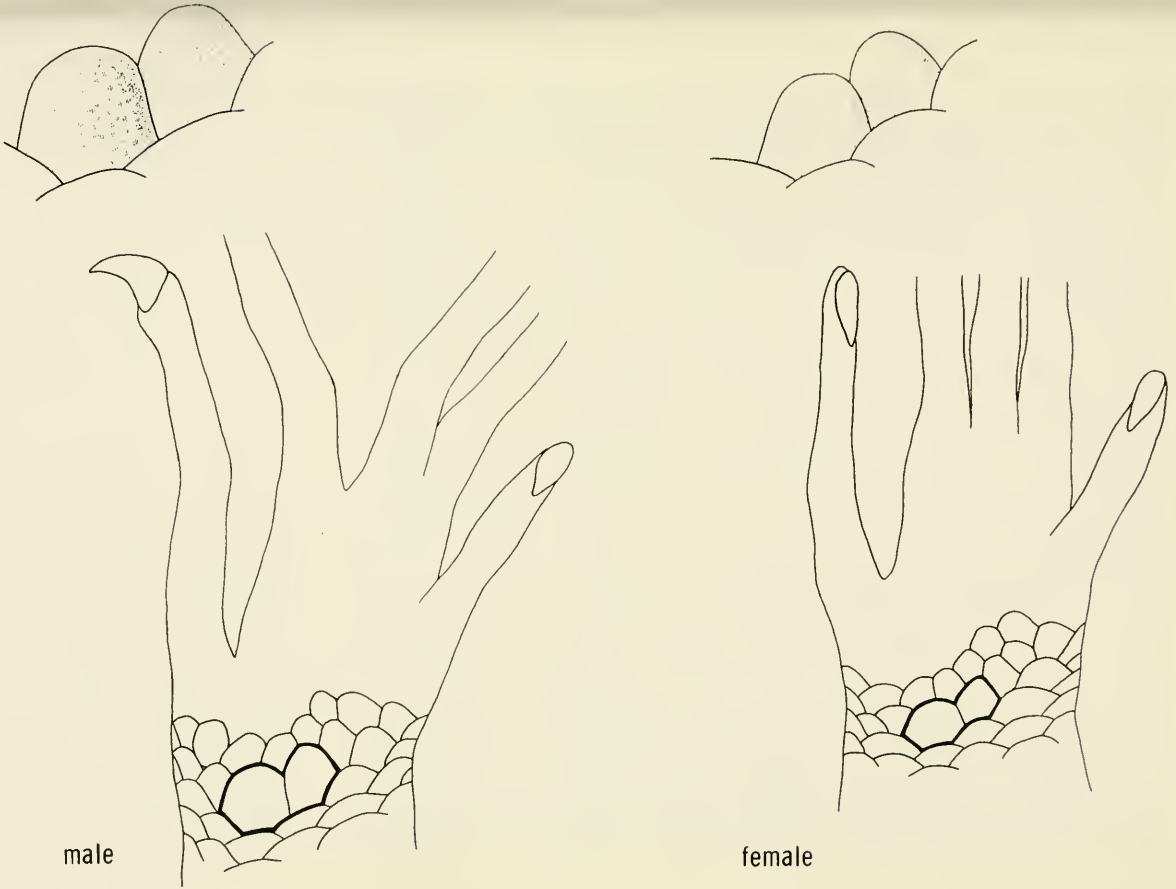

FIGURE 4. A comparison of the "heel" scales of a male (snout-vent length = 69 mm) and female (snout-vent length = 64 mm) *Apterygodon vittatus* from the Baram District, Sarawak.

only one major line of lygosomine evolution, i.e., that it has evolved more than once, is suggested by two lines of evidence. First, the process is variably developed in its anterior extent in species that are clearly closely related, e.g., *Hemiergis* and the Australian alpha *Leiolopisma,* and second, even those major groups which show a consistently strongly developed process articulating with the palatine often have very little else in common and, in some cases, are quite distantly separated geographically (Table 2). Thus not only has the process evolved independently in *Apterygodon,* but it has also done so in several other lygosomine lines as well. Again, like so many other skull characters that seem to have some taxonomic importance, we have no information about the function of the ectopterygoid process in these skinks. Presumably it may have something to do with skull kinetics, which in turn may have something to do with feeding habits. In any event, once the function of the process is known, its evolutionary significance and, therefore, its taxonomic significance should become clearer.

Zoogeography. The Bornean distribution of *Apterygodon* fits with the hypothesis of the close relationship of *Apterygodon* and *Dasia,* for Borneo is in that area of the Oriental Region where *Dasia* seems to have had much of its evolutionary history.

TABLE 2

Lygosomine taxa which are apparently only distantly related but which as groups show strongly developed ectopterygoid processes.

Group	*Area of Evolution*
1.) *Ctenotus, Egernia* (most species), *Tiliqua, Corucia, Tribolonotus*	Australian Region
2.) *Leiolopisma virens, L. flavipes, L. prehensicauda, L. semoni*	Australian Region
3.) *Tropidophorus* (some species)	Southeast Asia, Philippines
4.) *Solomonis* subgroup of *Sphenomorphus* (see Greer, 1967a)	Australian Region
5.) *Macroscincus* (see Hoffstetter, 1949)	Cape Verde Islands

Lamprolepis Fitzinger

Lamprolepis Fitzinger, 1843, Systema Reptilium, p. 22 (Type species: *Scincus smaragdina* Lesson, 1830, by monotypy).

Keneuxia Gray, 1845, Catalogue of the Specimens of Lizards in the Collection of the British Museum, p. 79 (Type species: *Scincus smaragdina* Lesson, 1830, by monotypy).

Diagnosis. On the basis of its palatal characters (Fig. 1) and the single large pair of nuchal scales bordering the parietals, *Lamprolepis* is an alpha skink (Greer and Parker, 1968). Most alphas, however, have either 11 premaxillary teeth (e.g., *Anotis, Emoia, Eugongylus,* most Australian and Pacific *Leiolopisma* and *"Sphenomorphus" bignelli, "S." minutus* and *"S." pseudornatus*), or a spectacle in a movable lower eyelid, or permanent brille (e.g., all alpha *Leiolopisma* and *Ablepharus*). They can thus be distinguished from *Lamprolepis,* which has but 9 premaxillary teeth and a scaly lower eyelid. In these two characters *Lamprolepis* is similar to the primitive alpha genus *Mabuya;* in fact, the only way *Lamprolepis* can be readily distinguished from all *Mabuya,* except the most geographically distant species in tropical America (exclusive of *M. atlantica*), is by the absence of keels on the body scales.

The only other alpha taxon not mentioned above is the African *Eumecia.* This genus encompasses one or two attenuate species with a reduced number of digits and is easily distinguished from the more robust, pentadactyl *Lamprolepis.*

Referred species. nieuwenhuisi Lidth de Jeude, 1905; *smaragdina* Lesson, 1830; *vyneri* Shelford, 1905.

Distribution. Two of the three species, *nieuwenhuisi* and *vyneri,* are confined to Borneo, whereas *smaragdina* is very widespread. This species occurs from Formosa, the Philippines, Palawan and the Sulu Archipelago, the Celebes and Lombok (but not Bali or west) south and east through Micronesia (Palau Islands and the Carolines east to the Marshalls), the Indo-Australian Archipelago, New Guinea and Cape York (Australia) to the Solomon Islands

and the Santa Cruz Islands.[1] In the Indo-Australian Archipelago south of the Philippines, the western limit of *smaragdina's* distribution follows Wallace's Line exactly (see fig. 7 on page 167 in Mertens, 1930).

Reproduction. L. smaragdina is the only species in the genus for which information about reproduction is available, and from all accounts (Hediger, 1934; Alcala, 1966; and Fred Parker, personal observation) as well as my own observations, it is clear that the species consistently lays but two eggs in a clutch.

The eggs are laid inside the rotten wood and rubbish in hollow branches and trunks (Fred Parker, personal observation), in the "moist humus collected in rotting parts of tree trunks, exposed roots, and points of intersection of main tree trunks . . . in nesting sites . . . very close to or several meters above the ground" (Alcala, 1966) or, probably less frequently, on the ground under logs or stones (Hediger, 1934).

Brown and Reyes (1956) found that the maximum incubation period for *smaragdina* in the Philippines was 54 days, while Parker reports that "an egg laid on 1 October . . . hatched on 27 November," indicating an incubation time of approximately 58 days.

Field notes. L. smaragdina is one of the best known lizards in the Pacific. This notoriety is undoubtedly due to the species' great abundance, its medium-large size and beautiful coloration, and its propensity for the more or less bare parts of tree trunks. In an effort to incorporate the best known aspects of the lizard's ecology and behavior, I have chosen for presentation below the accounts of four people, each of whom has seen *smaragdina* in the field in a different part of its range.

[1] Reports of *L. smaragdina* from Java and Borneo (de Rooij, 1915) are probably in error. Mertens (1929) says that the species is certainly absent from Java and attributes its inclusion in the Javanese fauna to a kind of thoughtless recording of locality that was apparently fairly usual in regard to species actually native to more eastern islands in the Indo-Australian Archipelago.

The single specimen on which the Bornean locality is based is not *L. smaragdina* but *L. nieuwenhuisi* (Mertens, 1929; Brongersma, 1933), a species which is endemic to Borneo. Furthermore, Dr. Robert Inger, who has been involved in recent studies on the herpetology of Borneo, writes (letter of 17 July 1968): "So far as I know, *Dasia smaragdina* does not occur on Borneo. I have never seen any specimens in any museum here or in Europe with a Bornean locality."

According to Hediger (1934), who worked primarily in the Bismarck Archipelago and in northern New Guinea, *smaragdina* lives primarily in isolated trees, small groups of trees, and on the forest edge. It is most usually found on tree trunks and resorts to the tree branches only for protection from the rain and on cloudy days. The lizard is extremely arboreal in its activities and apparently descends to the ground only for an occasional insect and sometimes to lay its eggs. When approached by an intruder, these skinks characteristically scurry around to the other side of the tree trunk just as squirrels often do. Although primarily insectivorous, some individuals examined by Hediger had masses of leaves and flowers in their stomachs.

In the Philippines *smaragdina* "has been found in dipterocarp, freshwater swamps, and mangrove forests, wooded grasslands, and coconut groves. It prefers areas with big trees that are exposed to the sun, irrespective of the amount of ground cover. Its altitudinal distribution is from sea level to about 600 meters" (Alcala, 1966).

Fred Parker, speaking of *smaragdina* on Bougainville and its neighboring islands in the Solomons, says that it is "mainly an arboreal species but during the day some can be found feeding on the ground in undergrowth. When they are disturbed they run to the nearest tree trunk. The preferred trees are those without thick creeper growth, such as coconut palms and breadfruit trees. The species is more common in open cleared areas, on trees still standing in gardens, and in small coconut plantings. In thick primary forest they are rarely seen. Found all over the lowlands and into the mountains but not very common over 2000 feet, except perhaps in the Guava area."

Marshall (1951) had the opportunity of observing *smaragdina* on the extreme northeastern periphery of its range on the islets of Arno Atoll in the Marshall Islands. He noted that here "this strictly arboreal skink is the diurnal counterpart of the Big Tree Gecko [*Gehyra oceanica*], and one or two can be seen on almost every coconut trunk during their hours of activity from about 7:30 a.m. to 5 p.m. (if sunny). They may remain motionless for long periods, pressed against the clear trunk, with the head held out at an angle. On uninhabited islands where there is denser vegetation, they will come lower in the leafy understory of vines and shrubs but are rarely found on the ground. They occur on just about all the islets of the atoll; though . . . none [were found] on Autore, one was seen on tiny Rakijer, much smaller than Autore, and containing only 3 or 4 coconut palms. A little

islet next to Rakijer, which had only a growth of *Scaevola,* lacked any lizards of any kind. . . . [*Smaragdina*] sleeps at night on the trunk, wherever they happen to be at the end of the day, as evidenced by the fact that individuals will seldom be roosting at the same spot on successive nights."

In contrast to this vast amount of information for *smaragdina,* we know virtually nothing about *nieuwenhuisi* or *vyneri.* According to M. A. Smith (1931), two *nieuwenhuisi* were collected at 3000 feet on Mt. Kinabalu, North Borneo, and a *vyneri* in the Field Museum was collected 8 feet up a tree in forest.

Relationships within the genus. The two Bornean species of *Lamprolepis, nieuwenhuisi* and *vyneri,* are extremely closely related, perhaps even conspecific, and both are seemingly more primitive than *smaragdina.* Both *nieuwenhuisi* and *vyneri,* for example, have retained supranasal scales, whereas *smaragdina* has lost them; *nieuwenhuisi* and *vyneri* also lack the single enlarged heel scales characteristic of male *smaragdina* (Gandolfi, 1907, and Fig. 5, this paper), and in this lack the two species may also be primitive.[1]

Within *smaragdina* itself Mertens (1929) has suggested that the Moluccas "subspecies," *moluccarum,* is the most primitive living population. This argument was based on two lines of reasoning: first, this population is more or less centrally located in regard to the other named populations of *smaragdina* and can therefore be looked upon as occupying a central area from which the species could have dispersed evenly in all directions, and second, the light grey to greyish brown ground color of *moluccarum*—in contrast to the unusual (for skinks) green color in most other named forms

[1] Although the single enlarged heel scale of male *Lamprolepis smaragdina* is very similar to the paired enlarged heel scales of *Dasia* and *Apterygodon,* even to the point of having a glandlike appearance, the scales have probably differentiated independently in each group. The best evidence for this lies in the fact that the nearest living relatives of the two groups' common ancestor, i.e., the primitive southeast Asian *Mabuya* (see below), lack such highly differentiated heel scales. An histological examination of the scales' morphology and perhaps a chemical analysis of the cell products (if the scales are glandular) would make an interesting extension of the comparison of these heel scales.

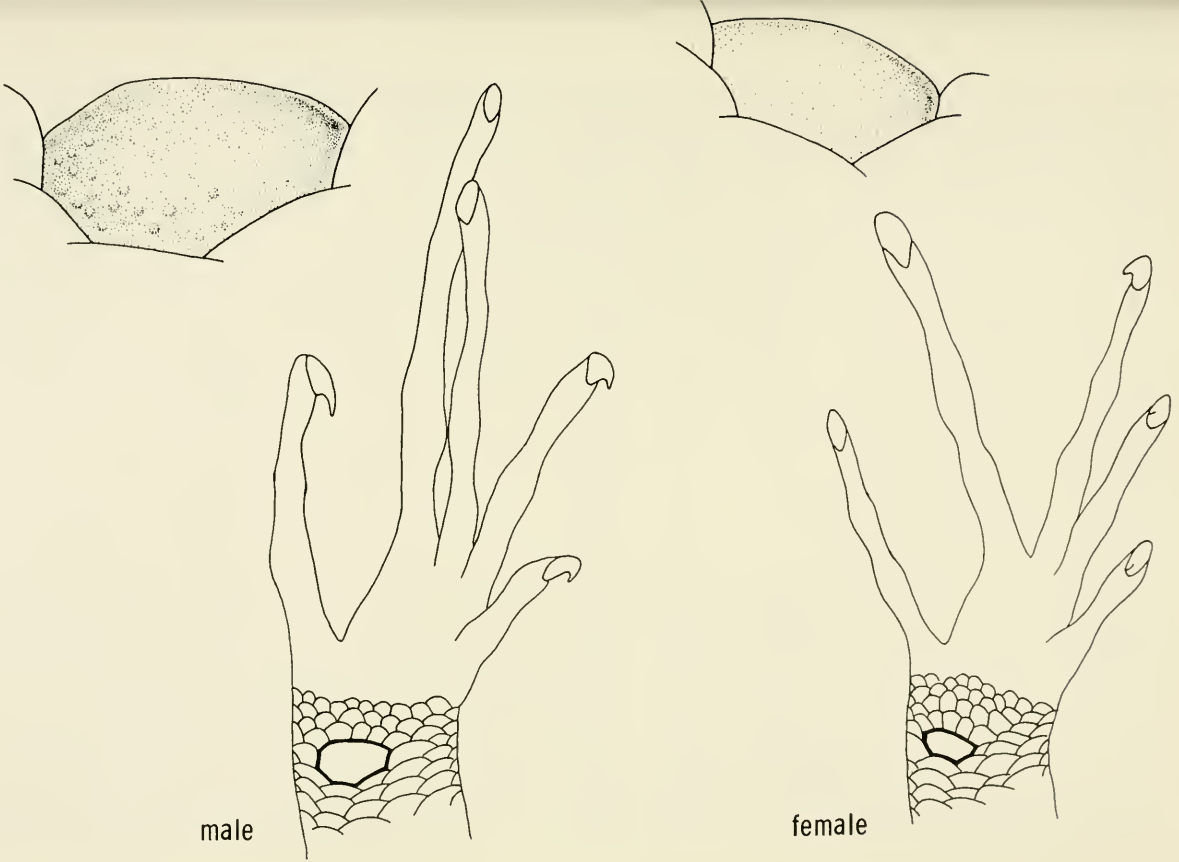

FIGURE 5. A comparison of the "heel" scales of a male (snout-vent length = 86 mm) and female (snout-vent length = 83 mm) *Lamprolepis smaragdina* from Bougainville, Solomon Islands.

of *smaragdina*[1]—is probably most similar to the drab ground color of most other ground inhabiting skinks that are presumably most similar to the ancestor of *smaragdina*.

As they stand, Mertens' arguments are overdrawn, but they do point the way; thus, while it is naive to place too much emphasis in pinpointing the geographically central area of a species as the center of its dispersal, I do think that the origin and early distribution of *smaragdina* is more likely to have occurred in the western part of its range, in an area close to its nearest relatives and well known as a source area, than in the remote Pacific island chains where *smaragdina* reaches its easternmost limits. And while it is probably true that a drab color pattern is more likely ancestral to a bright green one than vice versa, it is unnecessary to imply that the amount of green in a color pattern is strongly correlated with evolutionary age. In this more diffuse argument the two lines of evidence mesh as they were supposed to in Mertens' argument, for the subdued, more achromatic (primitive) color patterns are characteristic of the populations in the western part of the range, where, as I said, *smaragdina* probably first arose and from whence it dispersed, whereas the predominately green (advanced) color patterns are characteristic of the populations in the eastern part of

[1] All the attempts to name subspecies of *smaragdina* (Barbour, 1912 and 1921; de Rooij, 1915; Mertens, 1929) have relied heavily on differences in color pattern. This method, however, has several shortcomings. First, the taxonomically important greens and yellows are lost in preservation so that the remaining structural and melanistic color patterns are very unlike, and generally not correlated with, the patterns in life, and second, there is often a good deal more continuous variation, or possibly in some cases, discrete polymorphism, in single breeding populations than those who ascribe to the current subspecies concept of *smaragdina* would like to admit (some of this pattern variation in single breeding populations is described by Taylor, 1922; Hediger, 1934; Marshall, 1951; and Brown and Marshall, 1953).

This is not to say, however, that differences between populations of *smaragdina* do not exist. There are clear differences in color pattern between populations, but they are of a statistical nature and not absolute; also, judging from preliminary observation, there are discernible proportional differences between populations. Whether these differences can be worked out to the point of establishing a new subspecies concept for *smaragdina* is problematical, for the basic data-gathering task will be Herculean. In the meantime, however, and by way of taking a step toward unraveling this larger problem, there is a real need to understand the genetic and ecologic aspects of color pattern variation in populations of *smaragdina*.

the range, i.e., in the Pacific island chains, which are more likely to receive colonists than to send them.

I can add one additional piece of color pattern data to the argument that the western populations of *smaragdina* are generally more primitive than the eastern populations. This is the fact that in western *smaragdina* there is often a whitish, "paint brush" streak extending from the flank onto the base of the tail which passes directly over the back leg. This streak is also present in the Bornean *vyneri* and *nieuwenhuisi*, i.e., the closest living relatives of primitive western *smaragdina*, but it is absent in the *smaragdina* from the eastern part of the species range, i.e., in those populations derived from the more primitive western *smaragdina*. Presumably, therefore, the white flank stripe of *vyneri*, *nieuwenhuisi*, and primitive western *smaragdina* has been lost in the evolution of the advanced eastern *smaragdina*.

Relationships with other genera. Lamprolepis is most similar to *Mabuya* and differs from all the Old World species of this genus only in having smooth instead of keeled body scales. The New World species of *Mabuya* (except *atlantica*) also have smooth body scales but the great geographical distance between the smooth-scaled *Lamprolepis* and the smooth-scaled *Mabuya* argues for the independent evolution of this condition in both groups.

If one assumes that the most geographically proximate species of *Mabuya* are probably most like the ancestors of *Lamprolepis*, then the loss of pterygoid teeth has been another feature in the evolution of *Lamprolepis* from *Mabuya*. All southeast Asian *Mabuya* have pterygoid teeth, whereas the palatal teeth have been lost in all the New World species and in about half the African species, but in only one of the south Asian species (*bibroni*) examined to date. It looks, therefore, as if the pterygoid teeth, like keeled body scales, may have been lost independently in both *Lamprolepis* and the advanced species of *Mabuya*.

It thus seems that both *Dasia* (*sensu stricto*) and *Lamprolepis* are independently derived from a *Mabuya*-like ancestor, and they might, in fact, have shared the same ancestor. Since this time, however, the two taxa have diverged to a great extent. *Dasia* evolved a more extensive secondary palate (by incorporating the pterygoid bones), a slower gait, and an unusual juvenile color pattern but retained, as a primitive feature from its *Mabuya*-like ancestry, pterygoid teeth and keeled body scales. *Lamprolepis*, on the other hand, retained a basically *Mabuya*-like palate, gait, and color pattern (except in the greenish eastern populations of

smaragdina) but lost the pterygoid teeth and keeled body scales (and later the supranasal scales in *smaragdina*) of their *Mabuya* ancestry (Fig. 6).

Zoogeography. The significance of Wallace's Line to the zoogeography of *Lamprolepis* probably lies in its coincidence with the eastern edge of the Sunda Shelf, i.e., the eastern limit of the Asian land mass that would result with normal Pleistocene lowering of sea levels. With such lowering of sea levels, Borneo, the island harboring the two primitive species of *Lamprolepis,* would be connected to the Asian mainland along with Sumatra and Java, while the area to the east of this land mass, i.e., the area inhabited by the advanced species of *Lamprolepis,* would still be an archipelago, albeit with an increased average island size.

The dynamics of this distribution might have been somewhat as follows: The ancestor of *vyneri* and *nieuwenhuisi* probably arose from a primitive *Mabuya*-like skink on the land mass of the Sunda Shelf when this area was a dry extension of the southeast Asian mainland. This *vyneri-nieuwenhuisi* ancestor reached the island archipelago to the east of the Sunda Shelf and here gave rise to *smaragdina,* which then spread east with great success but which could not spread west back onto the dry land regions of the Sunda Shelf. The inability of *smaragdina* to spread westward onto the land of the Sunda Shelf was certainly not the result of an inability to cross water gaps, as its success in the east proves, but was probably due instead to an inability to penetrate the complex, basically mainland continental fauna of the Sunda Shelf land mass.

ACKNOWLEDGMENTS

I would like to thank first and foremost Mr. James P. Bacon, Jr., Dr. Walter C. Brown, Dr. Robert F. Inger, and Mr. Fred Parker for relating to me their field experiences with some of the animals discussed in this paper. Dr. Inger also very generously permitted me to examine two specimens of *Lamprolepis vyneri* in the Field Museum of Natural History. In addition, I have benefitted greatly from discussions with Mr. Ross Kiester about *Lamprolepis smaragdina* in Micronesia.

Dr. Ernest E. Williams of the Museum of Comparative Zoology has read the manuscript in several drafts and has offered many useful criticisms.

Mr. Ian T. Riddel took the photograph for Figure 2 and Mr. Laszlo Meszoly did the drawing for Figures 4 and 5.

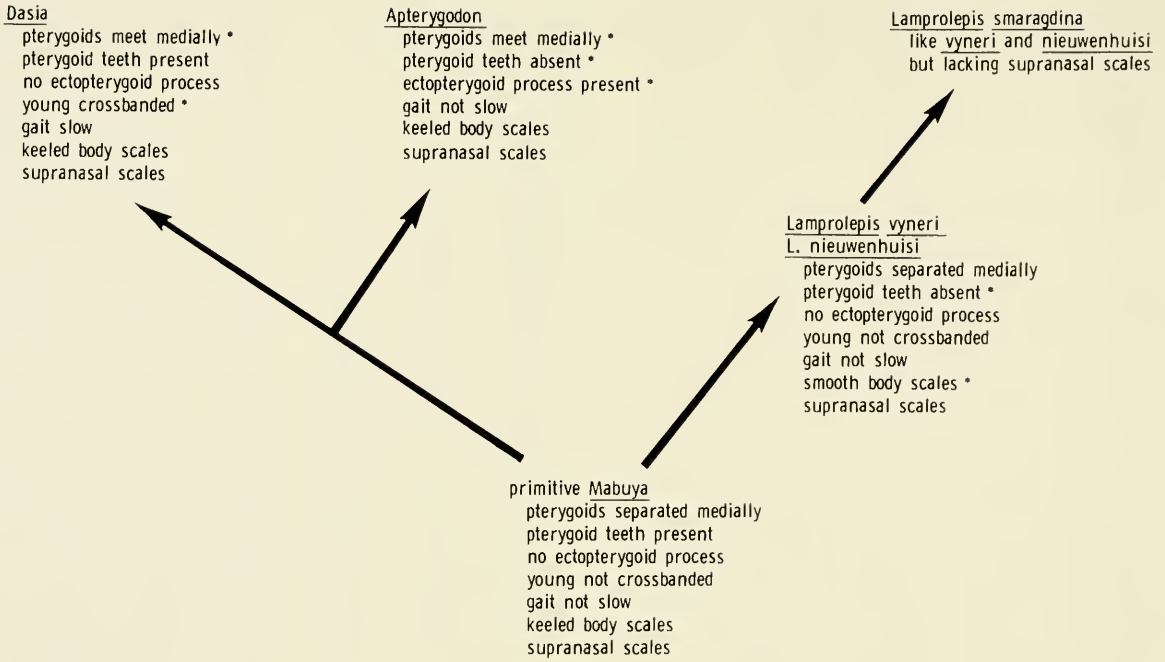

FIGURE 6. A hypothetical phylogeny of *Apterygodon*, *Dasia* and *Lamprolepis*. An asterisk (*) indicates a change in the character state of the derived taxon from that of the ancestral taxon. The young of *Apterygodon* being unknown, there is no information on their color pattern.

Work for this paper was carried out while I was first a National Science Foundation predoctoral and then later a postdoctoral fellow. An NSF grant to Dr. Williams (GB 6944) also provided funds for the completion of the paper.

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CAMBRIDGE, MASS. 15 MAY 1970 NUMBER 349

The Structural Niche of *Anolis scriptus* on Inagua

Anthony L. Laska [1]

ABSTRACT. The only member of its genus on Inagua Island, Southern Bahamas, *Anolis scriptus leucophaeus*, is believed to be derived from *A. cristatellus* of Puerto Rico, which shares the latter island with 10 congeners. As has been demonstrated in the case of other "solitary" anoles on other islands, *A. scriptus* has a broader niche than its ancestor on a multi-species island.

INTRODUCTION

Differences in structural niche among sympatric species of *Anolis* in the West Indies have been described recently by several authors (Collette, 1961; Ruibal, 1961; Rand, 1962, 1964; Schoener, 1968). The significance of intraspecific sexual dimorphism and its ecological relationships has been discussed by Rand (1967), Schoener (1967), and Schoener and Gorman (1968). Rand and Rand (1967) suggest that the lone species of anole on Curaçao, *Anolis lineatus*, occupies a somewhat broader structural niche than most species of the Greater Antilles. Similar field observations were made of *Anolis scriptus*, which occurs with no congeners on Inagua. Results of a six-day stay in February of 1967 suggest a fairly broad niche for this species, as for *lineatus*.

Anolis scriptus leucophaeus is a medium-sized anole. The mean of the largest third of all male specimens examined was 67.6 mm ($n = 36$) in snout-vent length, while corresponding females averaged 46.3 mm ($n = 70$). The closest relative of this species is *A. cristatellus cristatellus* of Puerto Rico (Gorman et al., 1968).

Great Inagua is located about 110 km north of Haiti, approximately 100 km from easternmost Cuba. About 70 by 30 km, it is predominantly flat, the highest point being East Hill at 40 meters. Lower hills dot the eastern half of Inagua's coastline. A large,

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shallow, saline lake fills a substantial area in the western interior of the island, and brackish mud flats are common. Inagua receives little rain, a yearly mean of 612 mm; and the annual temperature range is 22 to 30°C.[1] Cactus, thorn scrub, and low bushes are common in the dry flatlands, while stands of buttonwood and larger trees are found on low-lying ground. Sizeable palmetto groves occur on low aeolian hills along the shores in the regions studied to the northwest and south.

The low profile of Inagua indicates that this island is relatively young. This young age, combined with the movement of currents toward the northwest and the presence of submerged island banks between Puerto Rico and the southern Bahamas, accounts for the close relationship between the *Anolis* faunas of Puerto Rico and Inagua (Gorman et al., 1968).

FIELD METHODS

For this study anoles were observed and collected in western and southern parts of Great Inagua and on Sheep Cay, off Northwest Point. They were found most frequently in palmetto groves and stands of large trees but were rarely seen in thorn scrub, although several sub-adults were observed in dense patches of cactus and adder's tongue in Matthew Town. No apparent intraspecific variation was found among *scriptus* collected on Inagua proper or when these were compared with specimens taken from Sheep Cay.

To determine perch preference of this species, perch height and diameter were recorded for anoles observed at five principal localities: Northwest Point, Sheep Cay, Matthew Town, and neighboring areas of Salt Pond Hill and Conch Shell Hill. A total of 168 individual observations was made with an effort to avoid repetition. All but 23 entries were seen on trunks of palmetto trees and trunks and branches of larger trees. Those exceptions were in clumps of cactus, on stumps, stone walls, fences, and major trunks in brush piles. The exceptions are not included in calculations.

RESULTS AND DISCUSSION

Most of the lizards recorded were perched above ground level and below 12 feet. The data in Table 1 suggest this species distributes itself vertically as a function of sex and size of individuals.

[1] These are means of the extreme temperatures between 1954 and 1968.

With four zones available (following Rand, 1964), 59 percent of adult males were observed between 6 and 10 feet, 68 percent of adult females perched between 3 and 5 feet, while 74 percent of juveniles were seen within 3 feet of the ground. Several juveniles were found on the ground or in leaf litter. Results of X^2 tests show that adult males were found significantly higher ($34>5'$; $22<5'$) than adult females ($4>5'$; $33<5'$; $P<.001$). Adult females occurred significantly higher ($29>3'$; $8<3'$) than juveniles ($5>3'$; $14<3'$; $P<.001$).

Table 2 compares *Anolis scriptus* with *A. lineatus* of Curaçao (Rand and Rand, 1967), both of which occur with no congeners. Rand's (1964) figures for the structural niche of *A. cristatellus cristatellus* are included for comparison between *A. scriptus* and its nearest relative. The vertical distribution of *scriptus* is nearly as broad as that of *lineatus* but its preferred perch diameter appears more restricted. Perch diameter limitation for *scriptus* is probably a reflection of the species' association with palmetto trees, which are prevalent on much of the island. Since the typical palmetto trunk measured 3 inches, a high number of entries for *scriptus* is found in the 1/2-3 inch column in Table 2. Uniformity in available perch diameters is reflected by a lack of statistical significance for comparisons of preferred perch diameter for *scriptus* males, females, and juveniles in Table 1.

Total height of the perch was incidentally recorded for 41 of the observations and the ratio of perch position to total tree height was calculated. Means for these ratios are given in Table 3 for males, females, and juveniles. Since most of the trees in the localities did not exceed 12 feet, those over 12 feet were eliminated in calculating the second series of figures; the ratios being based on 22 remaining individuals.

When tree heights of 12 feet and less are considered, the position of lizards relative to the tree crown is higher than when taller trees are included, as indicated by a substantially greater ratio for the former. Although an optimum perch height relative to the ground is suggested by these data, the inherent bias of the observer's position may have some influence.

Of the juveniles observed, 74 percent were less than three feet above ground level, away from most of the larger adults that might try to catch and eat them. Since these juveniles are not competing for food with many larger anoles, they have a better chance of developing faster in this niche (Rand, 1967).

Scriptus, as a solitary anole, occupies a broader structural niche than typical species occurring with congeners. But its niche is not nearly so broad as that filled by the totality of a mixed *Anolis* fauna (Rand, 1964).

ACKNOWLEDGMENTS

I thank E. E. Williams for several critical readings of the manuscript, numerous useful comments and continuing interest. I am also grateful to A. S. Rand, and G. C. Gorman and T. W. Schoener for critically reading the manuscript and making valuable suggestions. Thomas Schoener supplied measurement data for *A. scriptus.* Charles Bremer, of Morton Bahamas Limited, and J. R. Clackson, Chief Meteorologist of the Bahamas Department of Civil Aviation, provided climatic information for Inagua. I thank M. Hecht for helpful comments and Shirley Laska for assistance in the field and numerous discussions. Field work was supported by Grant GB-6944 to E. E. Williams.

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(Received 15 March 1970.)

Table 1. Structural niche of *Anolis scriptus*.

Number of Individuals Recorded

Perch diameter	Adult males				Adult females				Juveniles				Smaller individuals*				Total**			
Perching height	>3	½-3	<½	Tot.	>3	½-3	<½	Tot.	>3	½-3	<½	Tot.	>3	½-3	<½	Tot.	>3	½-3	<½	Tot.
>10′		1		1		1		1					2	1		3	2	2		4
6-10′	11	22		33	2	1		3		1		1	2	10	1	13	13	32	1	46
3-5′	6	12	1	19	7	18		25	1	3		4	11	30		41	17	42	1	60
<3′	1	2		3		7	1	8	3	10	1	14	6	24	2	32	7	26	2	35
Total	18	37	1	56	9	27	1	37	4	14	1	19	21	65	3	89	39	102	4	145

* Adult females plus juveniles plus unidentified individuals under two inches in snout-vent length.
** Adult males plus smaller individuals.

Table 2. A comparison among *Anolis scriptus* of Inagua, *A. lineatus* of Curaçao, and *A. c. cristatellus* of Puerto Rico.

Percent of Number of Each Species Recorded

	Perch height				Perch diameter		
	<3 ft.	3-5 ft.	6-10 ft.	>10 ft.	>3 in.	½-3 in.	<½ in.
Inagua *scriptus*	24%	41%	32%	3%	27%	70%	3%
Curaçao *lineatus*	32%	33%	27%	7%	67%	31%	2%
Puerto Rico *cristatellus*	47%	40%	11%	1%	65%	27%	7%

Table 3. Ratio of perch height to tree height for *Anolis scriptus*.

Tree height	Adult males	Adult females	Juveniles
6 ft. - 26 ft.	.42	.37	.14
6 ft. - 12 ft.	.67	.41	.20

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FIMBRIA AND ITS LUCINOID AFFINITIES (MOLLUSCA; BIVALVIA)

Kenneth Jay Boss

ABSTRACT. *Fimbria* is the only surviving genus of the Fimbriidae, a family of bivalve mollusks that flourished during the Mesozoic. The conchological and anatomical features of *Fimbria* show that the family belongs to the superfamily Lucinacea and that it is closely allied to the Lucinidae. The systematic position of the Fimbriidae in relation to other lucinoid families is discussed, and a possible phylogeny for the superfamily is re-constructed.

INTRODUCTION

The relationship of the Fimbriidae with other lucinoid bivalves has been questioned by McAlester (1966), who suggested that additional anatomical and morphological data would be necessary before certain families, the Fimbriidae included, could be unequivocally assigned to the Lucinacea. It has been usual to include *Fimbria* and its fossil relatives in the Lucinacea (Dall, 1895; Thiele, 1935; Franc *in* Grassé, 1960; Eberzin *in* Orlov, 1960; Newell, 1965; Moore, 1969). Dall *in* Zittel (1900) considered the Fimbriidae an offshoot of the Lucinidae. The reason for this assignation was conchological, based on the structure of the dental and ligamental elements of the hinge of *Fimbria*. Anatomical characteristics supplementing the features of the shell allow the definite inclusion of the Fimbriidae in the Lucinacea.

The species of Recent *Fimbria* were reviewed by Lamy (1921) and Nicol (1950), and according to the latter there are only two living species, both distributed in the Indo-Pacific area. During the Mesozoic, particularly the Jurassic and Cretaceous, the genus *Fimbria* was rich in number of species and was widely distributed throughout warm and temperate seas (Pictet, 1855; Stoliczka, 1871). Both species-number and distribution dwindled during the Tertiary.

THE ANATOMY OF *FIMBRIA FIMBRIATA*

Mantle. The mantle is thin, translucent over much of its surface and open ventrally in an extensive pedal gape. Its edge is fringed with two rows of tentacles. It is fused anteriorly above the anterodorsal surface of the anterior adductor muscle (Fig. 1) and posteriorly, ventral to the incurrent aperture (Fig. 2). The fusion of the mantle lobes anteriorly is much like that in *Myrtea spinifera* (Montagu) as figured by Allen (1958, fig. 7c) and provides a broad anterior incurrent pathway by which water and suspended matter are drawn into the mantle cavity.

Muscles. The adductor muscles are large and are differentiated into 'quick' and 'catch' fibers. The posterior adductor muscle is irregularly oblong and rounded, whereas the anterior adductor is larger and subsemilunate, with the ventral portion wider or more extensive.

Siphons. Incurrent and excurrent apertures are developed posteriorly (Fig. 2). The incurrent opening consists of a simple rounded aperture, laterally flanked by two ridges of tentacles; ventrally, the muscular lobes of the mantle are fused to form a narrow

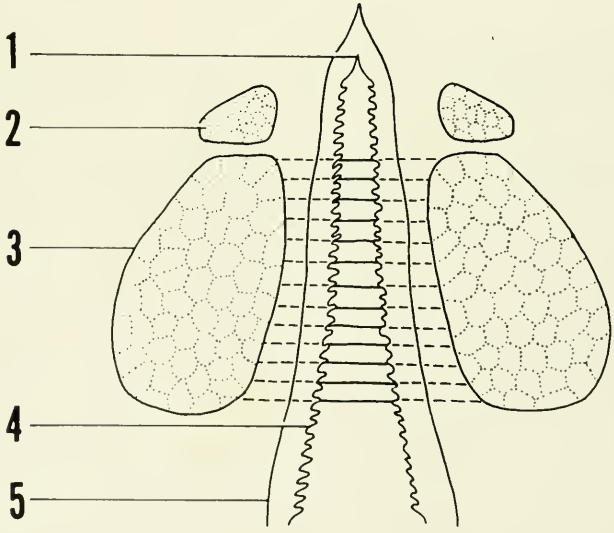


Figure 1. Diagrammatic view of anterior portion of *Fimbria*. 1. Point of anterior mantle fusion. 2. Anterior pedal retractor muscle. 3. Anterior adductor muscle. 4. Inner mantle fold. 5. Outer mantle fold.

isthmus, and dorsally they are joined in a broad union, which separates the excurrent siphon. The excurrent siphon consists of a large muscular tube which is capable of being invaginated and lies, when turned inside out, in the suprabranchial chamber. The siphonal retractor muscles are not developed, and the orifice of

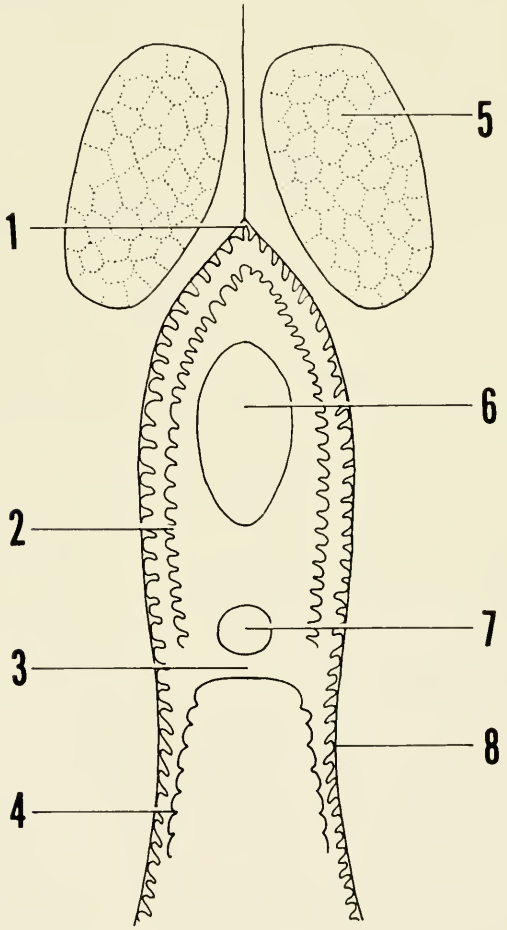


Figure 2. Diagrammatic view of posterior portion of *Fimbria*. 1. Point of fusion of outer mantle fold. 2. Secondary papillate fold. 3. Extent of tissue grade mantle fusion. 4. Inner mantle fold. 5. Posterior adductor muscle. 6. Excurrent invaginable siphon. 7. Incurrent aperture. 8. Outer mantle fold.

the aperture is flanked by two rows of papillae. The posterior aspect of *Fimbria* (Fig. 2) is similar to that of *Codakia orbicularis* (Linnaeus) as is illustrated by Allen (1958, fig. 9b).

Foot. The foot in *Lucina* has been studied by Barrois (1885). In *Fimbria*, it is large, subtrigonal, somewhat laterally compressed, longitudinally grooved or creased, heeled posteriorly, and pointed anteriorly (Fig. 3). In addition to its strong intrinsic longitudinal and circular muscles which surround a central sinusoidal lumen, the foot has a pair of anterior pedal retractors that attach to the shell just posterodorsal to the anterior adductor muscle and a pair of posterior pedal retractors that insert just anterodorsal to the posterior adductor muscle.

Gills and palps. The true gills or ctenidia consist of single, bilateral, inner demibranchs that are fused to the visceral mass dorsally and to each other posteriorly. They also attach to the muscular portion of the edge of the mantle between the ventral incurrent and dorsal excurrent apertures, thus effectively forming a septum that creates the dorsal suprabranchial chamber, into which empty the reproductive, excretory and faecal products.

Although longitudinally wrinkled, the gills are non-plicate, smooth or flat and apparently homorhabdic. They are thus similar to other luncinoids (Ridewood, 1903). In the specimens dissected, the demibranchs were retracted and thin, not thick and turgescent as are the gills in *Lucina* (Ménégaux, 1889). The filaments are interconnected, and the inner ascending lamella is shorter than the outer descending lamella, so that the latter appears to be a supra-axial extension of the demibranch. Unlike certain other lucinoids (Read, 1962; Hartman and Boss, 1966), the gills are not distinctively colored by hemoglobin.

As in other lucinoids (Thiele, 1886), the labial palps of *Fimbria* are very much reduced and consist of narrow flaplike lips bordering the mouth that accept, at their distal ends, the anteriormost portion of the demibranchs (Fig. 4). The reduction of labial palps is probably related to the increased efficiency of the ciliary mechanisms of the anterior incurrent canal and permits the ingestion of relatively large food particles (Allen, 1958).

The relation between the labial palps and ctenidia has been studied by Stasek (1963). Lucinoids, *Fimbria* included, exhibit a pattern, the category III of Stasek, in which the ventral tips of the anterior filaments of the inner demibranch are not inserted into a distal oral groove. Further, the inner demibranch may be fused to the inner palp lamella. Although the demibranch inserts

between the palp lamellae in *Fimbria*, there is no fusion (Fig. 4).

Mantle gills. The reduction of the true gills to only a single demibranch and the existence of the anterior incurrent canal probably were preadaptive anatomical features that aided in the development of another unusual character in lucinoids, namely, the mantle gill, noted by Duvernoy (1854: 115, pl. 5, f. 3) and Semper (1880).

Pelseneer (1911) discerned three different types of mantle gills and these have been discussed by Allen (1958). *Fimbria* is somewhat unusual in the development of two large flaps on the posteroventral surface of the anterior adductor muscle (Fig. 3). A large pallial vessel courses through the mantle diagonally from the mantle gill to the auricles. The flaplike structures of the mantle gills lie on either side of the channel of the anterior incurrent canal on the ventral surface of the anterior adductor muscle.

Intestine. The morphology of the alimentary canal was not studied in detail. A short esophagus enters the rather large stomach anteroventrally and the combined style-sac and midgut leaves it posteroventrally; the stomach is of the Type IV category of Purchon (1958). The digestive glands surround the stomach and are not developed into external visceral pouches. The intestine forms a simple loop in the visceral mass and enters the pericardium slightly to the right of the midline; the rectum passes over the dorsal surface of the posterior adductor muscle and empties into the suprabranchial chamber near the nephroprocts.

Heart and kidney. The complex of the heart and kidney is located posterodorsally and does not vary significantly from the typical eulamellibranch pattern (Ménégaux, 1890; Odhner, 1912). The heart is simple and lies in an expansive, somewhat triangular pericardium; two extremely large, thin-walled auricles receive blood from the large pallial vessel and the ctenidia. The ventricle is thick-walled and does not completely encircle the rectum; a dorsal aorta extends anteriorly. Pericardial glands (White, 1942) were not detected.

The kidney lies between the heart and the posterior adductor muscle and consists of two bilateral portions. The anteroventral reno-pericardial funnels collect fluid from the pericardial cavity; the posterior saclike parts of the kidney are broadly connected medially. The posterior portion of the kidney encircles the posterior retractor muscles. The kidneys open via bilateral nephroprocts to the suprabranchial chamber posterior to the gonadial aperture near the excurrent invaginable siphon.

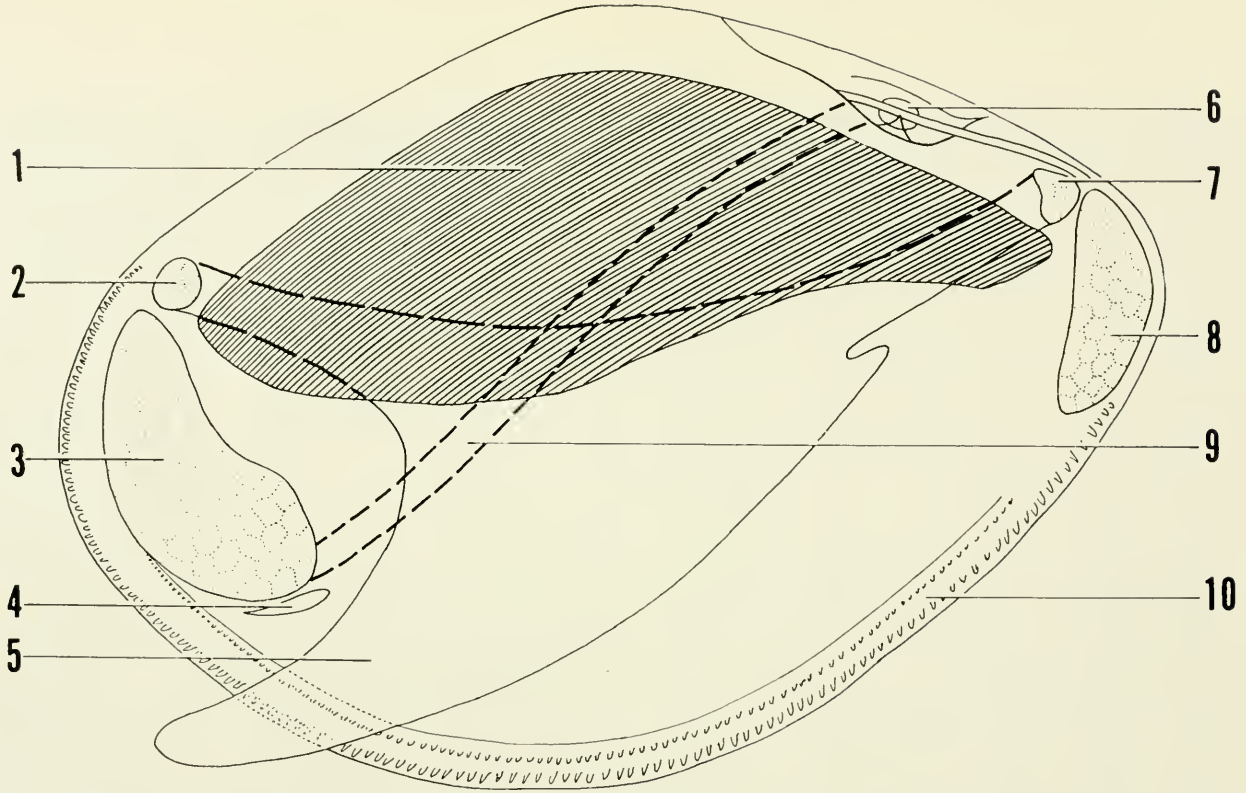


Figure 3. Diagrammatic illustration of the anatomy of *Fimbria*. Specimen viewed from left side with the mantle removed. 1. Ctenidium. 2. Anterior pedal retractor muscle. 3. Anterior adductor muscle. 4. Mantle gills. 5. Foot. 6. Pericardial area with rectum traversing the ventricle, lateral auricle and pericardium. 7. Posterior pedal retractor muscle. 8. Posterior adductor muscle. 9. Position of pallial vessel from the mantle gills to the heart. 10. Mantle edge with rows of tentacles.

Nervous system. The general pattern of the nervous system of *Fimbria* is not significantly different from that of other lucinoids or eulamellibranchs (Duvernoy, 1854). There are three main ganglionic centers: cerebropleural, pedal, and visceral. The cerebropleural ganglia are located on the inner surface of the anterior adductor muscle, just over the labial palps on either side of the mouth; they are united via a medial cerebropleural commissure (Fig. 4). Anteriorly, the ganglia give rise to nerves which supply

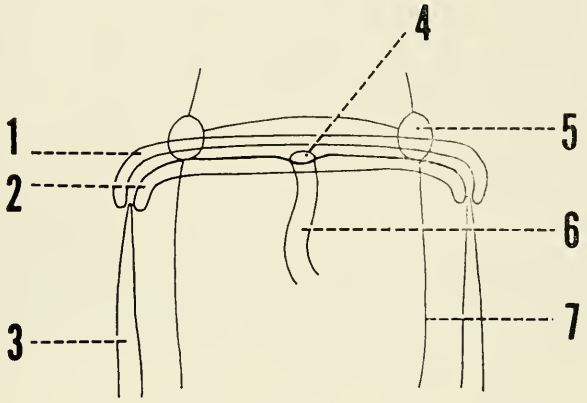


Figure 4. Diagrammatic view of the buccal area. 1. Outer labial palp. 2. Inner labial palp. 3. Ctenidium. 4. Mouth. 5. Cerebropleural ganglion with cerebropleural commissure. 6. Esophagus. 7. Cerebropleural-visceral connective.

the anterior adductor muscle and the anterior pallial musculature. Anterolaterally are branches to the labial palps, while extending ventrally from the ganglia are the cerebropleural-pedal connectives and posteriorly the cerebropleural-visceral connectives. Both pedal and visceral ganglia are closely juxtaposed and fused; the pedal ganglion gives rise to branches that innervate the intrinsic pedal musculature as well as portions of the viscera. The visceral ganglion is located on the inner surface of the posterior adductor muscle. Rather large branchial nerves arise laterally from the ganglion. The posterodorsal surface of the ganglion gives rise to small, short renal nerves, whereas the large posterior pallial nerve splays out over the ventral surface of the adductor muscle.

Specimens examined. (All *Fimbria fimbriata* (Linnaeus 1758)): Ifaluk Atoll, Caroline Ids. (USNM 616497); Bikini

Lagoon, Bikini Atoll, Marshall Ids. (USNM 584711); NE side of Ngaloa Ids., Fiji Ids. (USNM 674578); E of Mathuvata, N coast of Vanua Levu, Fiji Ids. (USNM 674577); Yanutha Id., N Coast of Viti Levu, Fiji Ids. (USNM 674576).

DISCUSSION

The unusual anatomical features in the Lucinacea were noted long ago by the famous naturalist Poli (1791), who figured the Mediterranean *Tellina* [*Lucina*] *lactea* with its elongate, cylindrical foot and single demibranch. Some of the anatomical characters of *Fimbria* were described by Valenciennes (1845a and b), who noted the reduction of the ctenidia to single demibranchs and the smallness of the labial palps. He showed that the foot of *Fimbria* differed in shape from that of other lucinoids. Thiele (1935), following Dall, remarked that in *Fimbria*, the mantle was fringed by two rows of papillae and the excurrent siphon was retractile. Allen (1958) studied a number of species of lucinoids and distinguished the Ungulinidae [Diplodontidae], Thyasiridae, and Lucinidae anatomically.

Table 1 contrasts the living families of the Lucinacea. The Fimbriidae are most closely allied to the Lucinidae. Both families have in common: 1) an excurrent siphon consisting of a unique invaginable tube; 2) an anterior point of fusion of the mantle edges that is dorsal to the anterior adductor muscle; 3) the ctenidia, consisting of a single inner demibranch on each side of the animal; 4) greatly reduced palps; 5) a tissue-grade fusion of the muscular lobes of the mantle ventral to the posterior incurrent aperture. Some species of the Lucinidae also develop accessory respiratory organs or mantle gills and have a foot which is differentiated posteriorly into a heel for digging. Fimbriids differ from lucinids in the development of a bilaterally compressed subtrigonal and pointed foot, thin demibranchs without large amounts of subfilamentar tissue, a double row of papillae along the mantle margin, and the confluence of the ventral surface of the anterior adductor muscle with the pallial musculature.

In addition, the shell of *Fimbria* is strong and heavy with thickened dentition, elongately-ovate in shape and cancellately sculptured (Fig. 5). The scar of the anterior adductor muscle is contiguous with the pallial line, a configuration unlike that of lucinids, in which the anterior adductor scar protrudes inwardly and is separated from the pallial line.

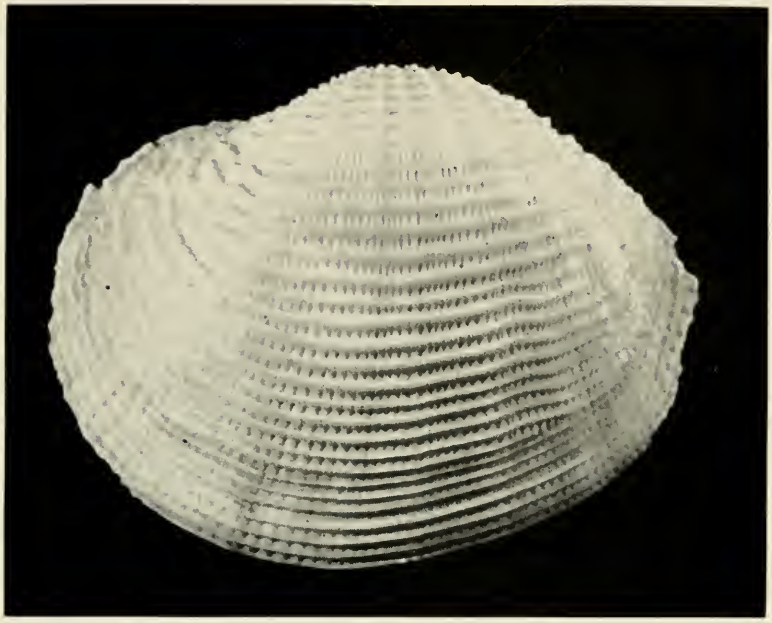


Figure 5. External view of left valve of *Fimbria fimbriata*, length = 30.5 mm, from Yanutha Id., N Coast of Viti Levu (USNM 674576).

Although the ecology of living *Fimbria* was not studied in the field, it is known that the species are reef-dwellers, preferring relatively shallow water in coralline sand (Nicol, 1950). The heavy, strongly ribbed shell is an adaptation to the coarse substrate which the species inhabits. Further, *Fimbria* probably lives near the sand-sea interface, for it possesses the anterior-posterior waterflow mechanisms of other lucinoids but lacks the vermiform foot to construct a long anterior incurrent mucus tube.

In addition to the family-level characteristics, *Fimbria* may be included in the Lucinacea because of the following anatomical features: 1) an extensive pedal gape; 2) the enlargement of the ventral surface of the anterior adductor muscle to facilitate an anterior inhalant current; and, 3) the relatively poorly differentiated and simple posterior incurrent aperture.

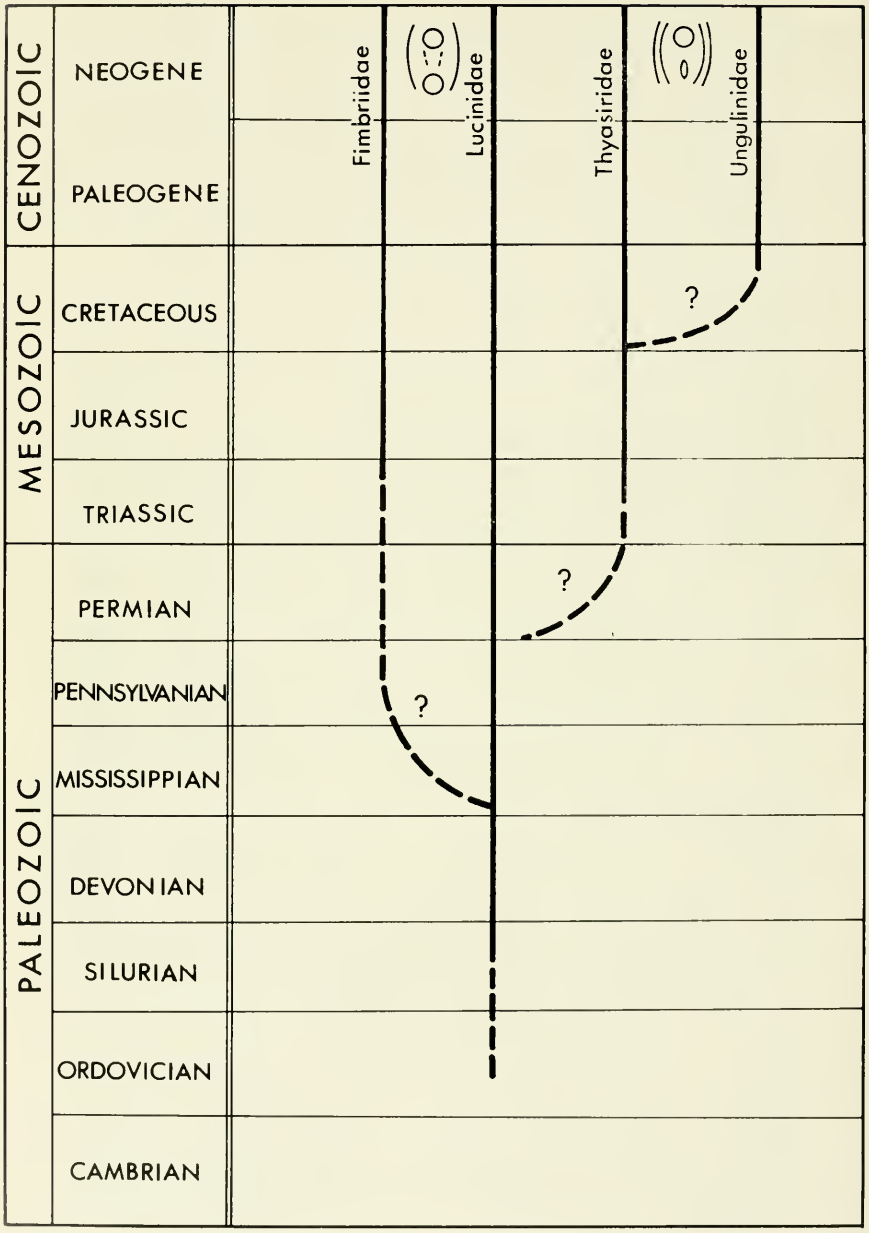
Table 1. Comparison of some anatomical features of four living families of the Lucinacea. EMF=Extent of mantle fusion beneath the incurrent aperture.

	Fimbriidae	Lucinidae	Thyasiridae	Ungulinidae
Anterior incurrent aperture	no fusion over anterior adductor muscle	no fusion over anterior adductor muscle	fusion ¼-⅓ surface of anterior adductor muscle	fusion ½-¾ surface of anterior adductor muscle
Posterior apertures	1) invaginable excurrent siphon	1) invaginable excurrent siphon	1) no siphon	1) no siphon
	2) incurrent aperture rounded	2) incurrent aperture rounded	2) incurrent aperture slitlike	2) incurrent aperture slitlike
	3) papillate	3) usually papillate	3) no sensory papillae; sensory "buttons"	3) papillate
	4) EMF tissue grade	4) EMF tissue grade	4) EMF not tissue grade	4) EMF tissue grade
Foot	subtrigonal, heeled	subvermiform, heeled	vermiform, not heeled	semipedunculate
Gills	inner demibranch only; not thick	inner demibranch only; thick	both outer and inner demibranchs; moderately thick	both outer and inner demibranchs; thin
Palps	much reduced	much reduced	reduced, but with maximum of seven folds	moderate, subtriangular
Digestive Diverticula	internal	internal	produced into external grapelike pouches	internal

The Fimbriidae are more distantly related to other lucinoid families. The Thyasiridae are unique in having a highly differentiated vermiform foot, external pouches for the digestive diverticula, both outer and inner demibranchs, a posterior incurrent slit without differentiated papillae, and a nontissue grade connection of the muscular folds of the mantle beneath the incurrent slit (Allen, 1958; Nakazima, 1958; Kauffman, 1967). The Ungulinidae [=Diplodontidae] possess posterior sensory papillae, both inner and outer demibranchs (Duvernoy, 1842), moderately sized labial palps, and a fusion of the mantle musculature over one-half the surface of the anterior adductor muscle.

Working with the Thyasiridae, Ungulinidae [=Diplodontidae], and Lucinidae, Allen (1958) suggested that these families were related in an evolutionary series, starting with the Ungulinidae [=Diplodontidae], which were considered the most 'primitive' family, and progressing through the Thyasiridae to the more 'specialized' Lucinidae. McAlester (1966) postulated that the relationship was actually reversed and that the Ungulinidae [=Diplodontidae] and Thyasiridae were convergent with 'typical heterodont' bivalves. The single important heterodont feature referred to by McAlester is the presence of both inner and outer demibranches in thyasirids and ungulinids; however, it is now known that this feature may not be as important as previously thought, since different species in the same genus (e.g., *Astarte*) may either have a full complement of demibranchs or have only a single demibranch. Nevertheless, if the Paleozoic stock of lucinoids had only a single demibranch, then the Ungulinidae [=Diplodontidae] and Thyasiridae, which branched from them in the late Paleozoic or early Mesozoic, had to re-acquire this morphological feature. Thus, McAlester's interpretation of the phylogenetic relationship among these lucinoid families is essentially correct. However, the geological record itself provides a better clue to phylogeny than do inferences based on supposed anatomical features of fossil lineages.

The Lucinidae and Fimbriidae are geologically older than the Thyasiridae and Ungulinidae [=Diplodontidae] (Moore, 1969) (Fig. 6). The lucinids may date from the Silurian; *Ilionia* Billings, a Middle to Upper Silurian genus from Sweden and eastern Canada is the first known member of the Lucinidae. However, if *Babinka* Barrande is considered a lucinoid (McAlester, 1965), the superfamily is traceable to the Middle Ordovician. *Fimbria* von Mühlfeld appeared in the Bathonian of the Middle Jurassic and radiated in the Cretaceous while other fimbriids were present earlier in the


CENOZOIC
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NEOGENE
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JURASSIC
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PERMIAN
PENNSYLVANIAN
MISSISSIPPIAN
DEVONIAN
SILURIAN
ORDOVICIAN
CAMBRIAN
Fimbriidae
Lucinidae
Thyasiridae
Unguliniidae
?
?
?

Figure 6. Proposed evolutionary relationships of four living families of the Lucinacea. Question marks indicate possible derivations of families. Solid lines denote known lineages: the Lucinidae, from the Silurian (*Ilionia* Billings); the Fimbriidae, from the Upper Triassic (*Schafhaeutlia* Cossmann); the Thyasiridae, from the Middle Triassic (*Storthodon* Giebel), and the Ungulinidae from the Upper Cretaceous (*Brachymeris* Conrad).

The diagrams indicate anatomical features: in the fimbriid-lucinid lineage, invaginable excurrent siphon, rounded incurrent aperture and inner demibranch only; in the thyasirid-ungulinid lineage, no excurrent invaginable siphon; slitlike incurrent aperture and both outer and inner demibranchs.

Upper Triassic (*Schafhaeutlia* Cossmann) and even in the Carboniferous (*Scaldia* de Ryckholt) (Eberzin *in* Orlov, 1960; Moore, 1969).[1]

The Ungulinidae [=Diplodontidae] probably arose in the Upper Cretaceous (*Brachymeris* Conrad and *Felaniella* Dall) and were certainly present in the Paleocene, whereas the Thyasiridae are known positively from the Cretaceous and probably from the Middle Triassic (*Storthodon* Giebel). Thus, the phylogenetic diagram presented by McAlester (1966) can be extended and augmented with the insertion of the Fimbriidae near to the Lucinidae, from which stem they diverged in the early Mesozoic or late Paleozoic (Fig. 6).

ACKNOWLEDGMENTS

Dr. J. Rosewater of the United States National Museum (USNM) loaned preserved specimens for dissection. The manuscript was critically read by Professor B. Kummel, Dr. R. D. Turner, and Mr. R. I. Johnson.

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[1] *Scaldia* de Ryckholt from the Visean and Tournaisian Dinantian of the Lower Carboniferous has only recently been placed in the Fimbriidae by Chavan *in* Moore (1969). Previously it was considered in the Edmondiidae (Vokes, 1967). Ryckholt's original figures indicate that *Scaldia* has a pallial sinus, a characteristic which prevents the genus from being considered Lucinacean and which removes it from the Fimbriidae.

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(Received 16 March 1970.)

ADDENDUM: While this paper was in press, J. A. Allen and J. F. Turner (1970. Pacific Science, **24**(2): 147-154) published 'The morphology of *Fimbria fimbriata* (Linné) (Bivalvia; Lucinidae)' in which they proposed placing the genus *Fimbria* in the family Lucinidae.

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